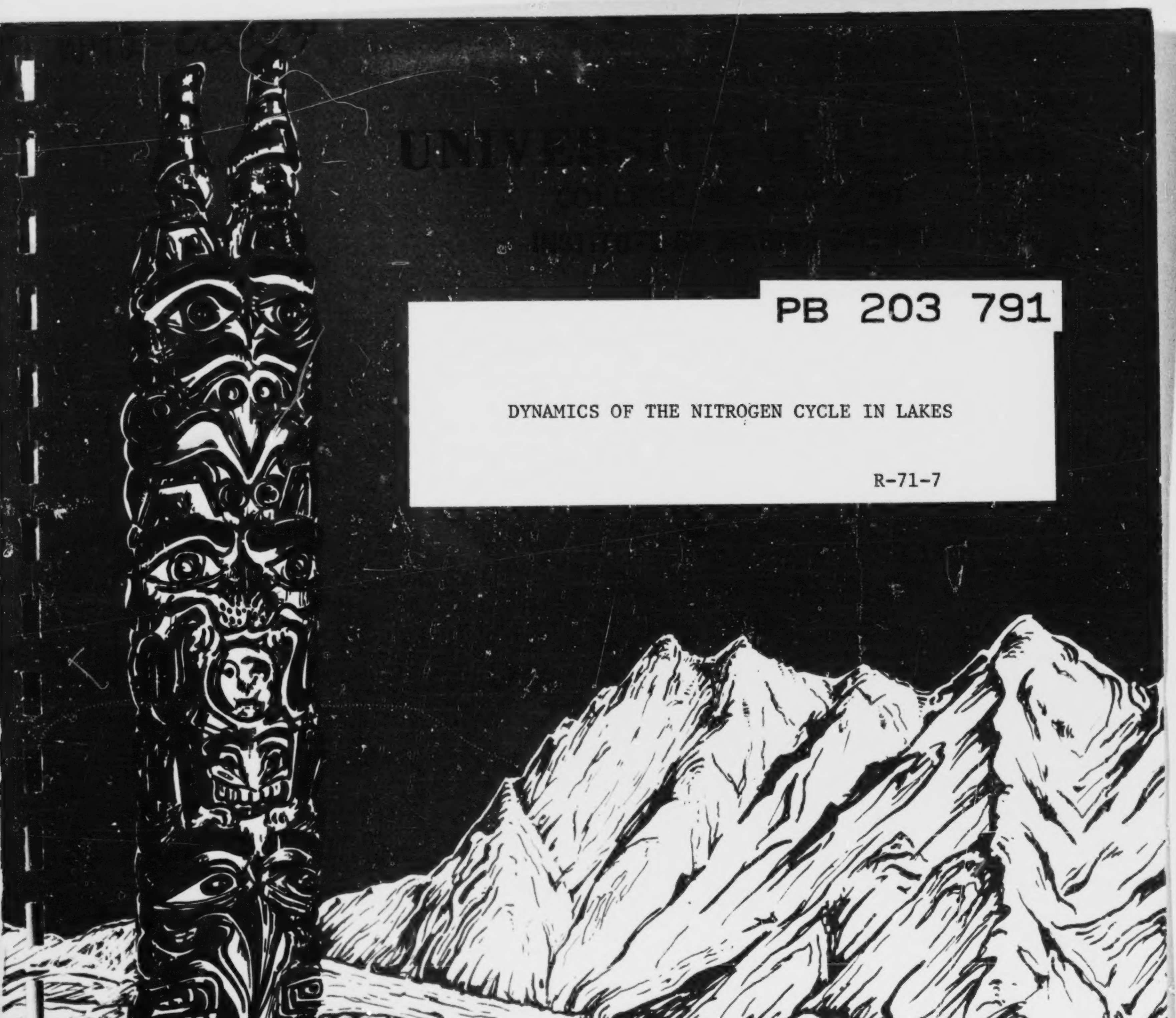

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DYNAMICS OF THE NITROGEN CYCLE IN LAKES

R-71-7

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16. Abstract

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3. Denitrification rates were measured accurately in anoxic lake waters.

4. Rapid ammonia supply and turnover was demonstrated in lake waters. This implies that substantial nitrogen regeneration takes place constantly in surface waters of these lakes, and that this can provide a major nutrient source for the photosynthetic population. Such ammonia supply is independent of any sediment interaction.

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INSTITUTE OF MARINE SCIENCE
UNIVERSITY OF ALASKA
COLLEGE, ALASKA

DYNAMICS OF THE NITROGEN CYCLE IN LAKES

Principal Investigator: Vera Alexander

Final Report to the Federal
Water Quality Administration
Grant No. 16010 DDS (formerly WP-00422)

Report Number R71-7
March, 1970

D. W. Hood
Director

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INTRODUCTION

The research initially supported by grant WP-00422 has been underway for several years, first under the National Institutes of Health and then under the Department of Interior, and over the period of years the objectives and goals have gradually shifted in response to the cumulative results. A complete final report thus cannot be given without some historical background.

The original aim during the initial funding period was to develop a method for measuring nitrogen fixation in natural waters using the heavy isotope of nitrogen ^{15}N. Although ^{15}N had been used in studies of protein metabolism and also for laboratory verification of nitrogen fixation by bacteria and blue-green algae, it had not yet been used in connnection with aquatic work. Our first measurements were made in some Alaskan lakes, with positive but unimpressive rates of nitrogen fixation detected (Dugdale *et al.*, 1959). Subsequent work on a Pennsylvania reservoir demonstrated high rates of fixation in connection with populations of blue-green algae dominated by *Anabaena* sp. (Dugdale and Dugdale, 1962). The method as developed during the course of this work is described in detail in Neess *et al.*, (1962). The next phase of the work on this reservoir involved extending the ^{15}N method to measurement of uptake rates of the two major inorganic nitrogen sources, nitrate and ammonia. This provided no additional technical problems, and the techniques for innoculation and incubation are similar to those used in the standard carbon-14 primary productivity work. The results obtained with this technique indicated a variable nitrogen uptake regime seasonally, with nitrogen fixation dominating in the late summer, and all three sources being used in the early summer. Ammonia was shown a very important nitrogen source for the phytoplankton (Dugdale and Dugdale, 1965).

At this point, the project was moved to the University of Alaska, and therefore the work was transferred to a lake in the vicinity of the University. The work was extended at this time to include other nitrogen transformations in adddition to uptake. For example, the rates of ammonia supply and turnover, of nitrification and also of denitrification were incorporated into the research plan. Here again, method development occupied a substantial proportion of the effort for a period of time. In addition, since nothing was known about lakes in interior Alaska, a considerable amount of basic limnological work was done. Complete nitrogen cycle work incorporated with a seasonal limnological study of Smith Lake was undertaken, including detailed work on the primary productivity regime. Here, again, nitrogen fixation was found a major input, but this time in connection with a single spring annual *Anabaena* bloom, with ammonia a major nitrogen source at all times. The complete annual cycle turned out to be interesting, with nitrate accumulating in the fall and winter, and then disappearing shortly after oxygen became depleted in the water under the ice in late winter. Using the ^{15}N method we developed for denitrification measurement, we were able to establish that this loss was due to denitrification (Goering and Dugdale, 1966). The nitrogen cycle and productivity information on Smith Lake formed part of a doctoral dissertation (Dugdale, 1965) and the nitrogen uptake data are given in Billaud (1968).

Work on the rate of supply of ammonia was intensified, using isotope dilution techniques. A highly variable but unexpectedly rapid turnover rate was indicated by this work (Alexander, 1970). On the other hand, nitrification rates appeared to be too slow to measure using the planned isotope techniques. The indications were that nitrification could not compete with uptake for the available ammonia during the summer months, and was only important in the absence of uptake in late fall and early winter.

Comparative sampling was carried out on a number of additional lakes, greatly expanding the range of limnological information available for Alaskan lakes. A small lake system in the Fairbanks vicinity, the Ace - Deuce Lake system was frequently included. The Tangle Lakes, a major lake system in the Alaska Range, was studied in terms of nutrient distribution. The Minto Lakes were visited on several occasions, and nitrogen fixation experiments were also carried out on hot springs within reach of Fairbanks with some results reported in Billaud (1967).

The aims of the work by this time included complete aquatic nitrogen cycling tracer studies, and in addition, we wished to attempt an evaluation of the importance of nitrogen fixation in as wide a selection of lake waters as possible. The method of Stewart *et al.* (1967) was added to the nitrogen fixation techniques used. This assay, based on the reduction of acetylene to ethylene by the nitrogen fixing enzyme, is very sensitive and much less costly than nitrogen-15 techniques, and if used judiciously in connection with nitrogen-15, can vastly increase the output of information.

The final facet incorporated into the work was studying the uptake of organic compounds. Since a great deal of work had been done on this program on the primary productivity rates in the lakes, we were also interested in the possible role of heterotrophy, since the lakes in subarctic Alaska are subjected to extensive dark periods. For this work, tritium labeled amino acids were used, and a radioautographic technique using stripping film was used to identify uptake by specific organisms. In addition, the uptake of carbon-14 labeled organics was used. A substantial portion of this work was carried out at the Naval Arctic Research Laboratory at Barrow.

MAJOR CONTRIBUTIONS FROM THIS PROGRAM

1. The importance of nitrogen fixation by blue-green algal populations was established, and nitrogen-15 was introduced for measuring *in situ* nitrogen fixation rates in natural waters.

2. Nitrogen-15 techniques were developed for measuring nitrate and ammonia uptake, and the importance of ammonia as a nitrogen source in lakes became apparent. The rates of ammonia uptake correlated well with primary productivity as measured using the carbon-14 technique.

3. Denitrification rates were measured accurately in anoxic lake waters.

4. Rapid ammonia supply and turnover was demonstrated in lake waters. This implies that substantial nitrogen regeneration takes place constantly in surface waters of these lakes, and that this can provide a major nutrient source for the photosynthetic population. Such ammonia supply is independent of any sediment interaction.

5. The limnological information available for interior Alaska has been expanded through this work, and there now exists a body of data which will prove invaluable for future work by our organization and by others.

6. The Dumas method using a Coleman nitrogen analyzer were introduced for preparing nitrogen samples for mass spectrometry (Barsdate and Dugdale, 1965).

RESULTS

Since many of the results have been published, or are currently available in manuscript form, this report will consist of a number of individual sections based on such manuscripts. The methods are incorporated into the various individual papers, and so will not be presented in a separate portion of the report.

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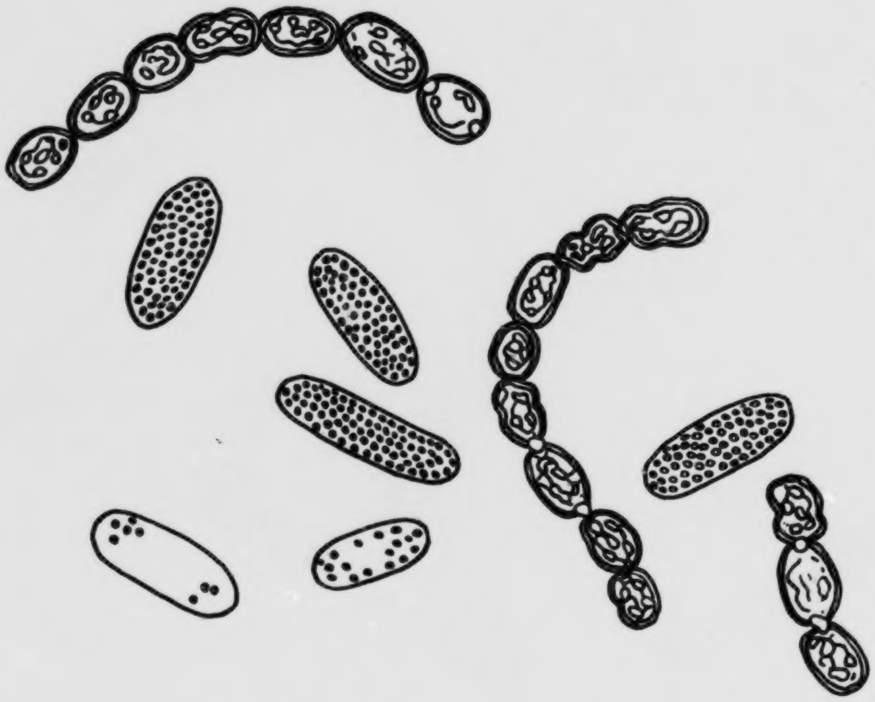
SECTION ONE

NITROGEN FIXATION

THE SMITH LAKE *ANABAENA* BLOOM

The annual bloom of *Anabaena flos-aquae* first reported in Dugdale, 1965, continues to be an annual feature of Smith Lake, and provides an ideal situation for studying bloom dynamics and also nitrogen fixation measurement technology. Two illustrations are included here showing stages in the annual cycle of the organisms. The bloom normally extends from June 5 to June 20.

Dugdale, V. A. 1965. Inorganic nitrogen metabolism and phytoplankton primary productivity in a subarctic lake. Ph.D. thesis, University of Alaska. University Microfilms, Ann Arbor, Michigan.



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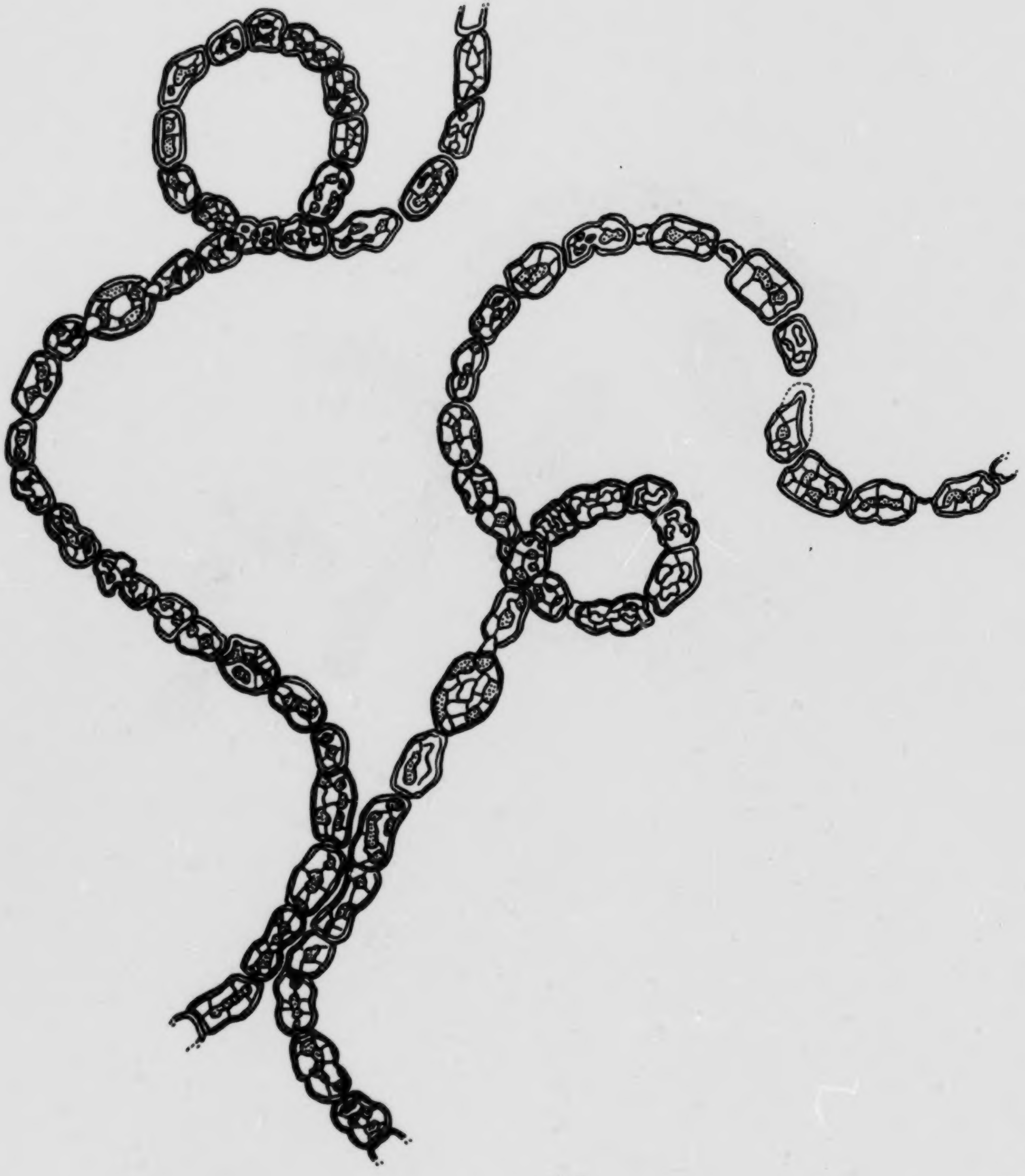
Nitrogen Fixing *Anabaena flos-aquae*, From Smith Lake, Alaska.
Terminal Part of Bloom Cycle, with Akinetes



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Nitrogen Fixing *Anabaena flos-aquae* from Smith Lake, Alaska During Early Stage of Bloom

Nitrogen Fixation and the Utilization of Other Inorganic Nitrogen Sources in a Subarctic Lake[1,2]

By Vera A. Billaud

Institute of Marine Science
University of Alaska, College, Alaska, USA

ABSTRACT

A year-round limnological study of the biological utilization of molecular nitrogen, ammonia, and nitrate in Smith Lake, a small subarctic lake in interior Alaska, showed that ammonia was consistently the most important nitrogen source. Of the two main algal production periods, the first took place under the ice in May, and depended on ammonia accumulated during the winter for a nitrogen source. The population at this time consisted largely of microflagellates. *Chlamydomonas, Euglena, Chlorella,* and *Mellamonas* were among the identified algae present. Immediately after the ice melted from the lake surface, a second population developed. These algae, consisting almost exclusively of *Anabaena flos-aquae*, used ammonia, nitrate, and molecular nitrogen simultaneously. During the remainder of the summer, uptake rates remained relatively low, with ammonia the most important nitrogen source; during the fall, nitrate uptake briefly approached the magnitude of ammonia uptake. ^{15}N tracer methods were used to measure the uptake rates in this work.

INTRODUCTION

In this paper, measurements of biological uptake rates of ^{15}N labeled ammonia, nitrate, and molecular nitrogen in a small arctic lake are discussed. The availability and utilization of nitrogen sources vitally influence, and perhaps at times control, the primary productivity of a lake. Since nitrogen undergoes a complex cycle in transport, very little can be assumed from information on the nutrient standing concentrations alone.

Measurements of instantaneous uptake rates of inorganic nitrogen nutrients have become possible using nitrogen compounds labeled with the stable isotope ^{15}N. In aquatic work, this technique was first applied to measurements of nitrogen fixation rates in fresh water. The method used was described in Neess et al. (1962), and the results of some of the first measurements are given in Dugdale and Dugdale (1962). In the latter paper, the importance of nitrogen fixation in the nitrogen nutrition of freshwater blue–green algae populations was confirmed. Previously, all observations of nitrogen fixation by algal blooms had been based on indirect evidence (see for example, Guseva, 1941; Utterback et al., 1942; Hutchinson, 1957).

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[1] Received for publication March 28, 1968.

[2] Contribution No. 28, Institute of Marine Science, University of Alaska. Based on a thesis sunmitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy from the University of Alaska, College, Alaska.

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After this preliminary confirmation with ^{15}N, further work was carried out confirming nitrogen fixation in fresh water (Goering and Neess, 1964), in coastal regions (Stewart, 1964, 1965), and in the open sea (Dugdale et al., 1964).

The first freshwater measurements of the uptake rates of ammonia, nitrate, and molecular nitrogen have shown that all three sources may be used concurrently (Dugdale and Dugdale, 1965). This is contrary to the widely held opinion that nitrogen fixation is facultative, and unlikely to persist where adequate supplies of the energetically more easily utilizable nitrogen sources, nitrate and especially ammonia, are available. The present study, part of a broader study of the biological nitrogen cycle in lakes, was designed to provide information on the relative importance of the three major inorganic nitrogen sources, and to investigate their seasonal patterns of utilization.

METHODS

A single station was selected for sampling. The depth at the station was 2.5 m, and a permanent buoy was placed for sampling and incubation of samples. For the nitrogen uptake work, samples were taken manually with a 2000-ml polypropylene beaker. The beaker was immersed to a depth of about 0.25 m. Samples for nutrient chemistry and oxygen were taken with a 500-ml Frautschy bottle.

Samples for measuring the uptake of nitrate or ammonia were directly introduced into 1000-ml pyrex reagent bottles, and the ^{15}N labeled ammonium sulfate or potassium nitrate was added from ampoules using a disposable hypodermic syringe. Each ampoule contained 2 μg-at of nitrogen with a known ^{15}N enrichment of 95, 97.5, or 99 atom %. In general, a total amount of nitrogen tracer equivalent to about 10% of the concentration of that form of nitrogen in the water was added. The enrichment was kept at this low level to eliminate the possibility of stimulation to growth from the added nutrient.

The technique described in detail by Neess et al. (1962) was used for the nitrogen fixation experiments. The sample was placed in a pyrex round-bottomed flask, with a 24/40 standard taper top. The volume used was either 500 or 1000 ml depending on the density of the organisms in the water. The gases in the water were removed by flushing with a 80–20 helium–oxygen mixture at slightly reduced pressure. This was accomplished by attaching the flask to a manifold via a specially designed sparger unit. After the sparging treatment, the manifold was evacuated and ^{15}N enriched nitrogen gas was added from a reservoir by displacement with a H_2SO_4–Na_2SO_4 confining fluid. This restored the pressure in the flask to atmospheric levels.

Incubation was carried out in situ by suspension from the sampling buoy and, during the 2nd year, also under standard light conditions in a constant temperature room at 20 C during the summer and 5 or 10 C during the winter, such that the in situ temperatures were approximated. Incubation times of 4 hr were used.

The post-incubation procedure consisted of filtering the water through a Hurlburt glass filter (984-H ultra filter; Reeve, Angel and Co.), after which the filter was dried. Mass spectrometry was carried out using a Bendix Time-of-Flight mass spectrometer (Model 17-210). The inlet system of this machine was connected via a liquid nitrogen trap to a modified Coleman Nitrogen Analyzer. With this system, conversion of the sample to nitrogen gas was carried out using the modified Dumas procedure described by Barsdate and Dugdale (1965). The mass 28 and mass 29 peaks were scanned on the mass spectrometer, and an Oskar K chart reader was used to transfer the peak heights to IBM cards. The following calculations were carried out on an IBM 1620 computer. The isotope ratios calculated from the mass 29 and mass 28 peaks were converted into atom percent values according to the formula:

$$A_f = \frac{100\,r}{2+r}$$

where A_f is the atom percent ^{15}N of the particulate material at the end of the incubation period. From this, the normal atom percent of unenriched nitrogen was subtracted. This value was determined by running isotope ratio determinations on unenriched filtered lake water.

The atom percent of the nitrogen supplied at the beginning of the experiment had to be known in order to calculate the amount of nitrogen taken up. In the case of nitrogen fixation experiments, in which all the unlabeled nitrogen was removed, it was simply the enrichment in the supplied gas. For the nitrate and ammonia uptake experiments, the amount of unlabeled nitrate and ammonia in the water had to be included in the calculation. The atom percent of the available nitrogen at the beginning of the experiment was designated A_1. The amount of nitrogen taken up during the experiment was then:

$$N_f = \frac{N_t \times A_f}{A_i}$$

where N_t is the total particulate nitrogen in the sample. This method of calculation is valid as long as the change in N_t during the experiment is very small. In practice, the change in N_t during a short-term experiment seldom exceeds 1%.

Particulate nitrogen was determined using a Coleman Nitrogen Analyzer on samples collected on Hurlburt glass filters. Chlorophyll *a* was determined spectrophotometrically after 24-hr dark extraction of the pigment in 90% acetone; a Beckman DB scanning spectrophotometer was used, and a method of calculation was adapted using the specific absorption for Chlorophyll *a* given by Bruinsma (1961):

$$\frac{\text{O.D. } 658 \times 14.9 \times \text{solvent volume}}{\text{Lake water volume filtered}} = \text{mg liter}^{-1}\text{Chl. } a.$$

The optical density at 750 mμ was first subtracted from the optical density at 658 mμ. The results obtained were a little lower than those obtained by Bruins's calculation method for total chlorophyll for the same water sample.

Nitrate was measured using a modification of the Mullin and Riley procedure (1955) similar to that described by Strickland and Parsons (1960). Internal standards were necessary for each sample, since the water color was highly variable and affected the sensitivity of the reduction step; small portions of a standard curve were run using the sample itself rather than relying on a distilled water standard curve. In addition, a 10-fold increase in the copper catalyst was required for the reduction of these samples, since the colored substance apparently complexed much of the added copper. For ammonia, the sodium phenate method of Riley (1953) was used after vacuum distillation or diffusion. The oxidation method of Richards and Kletsch (1964) was used for a few of the later analyses.

Oxogen was determined using the Alsterberg modification of the Winkler procedure, and *p*H was measured on a Beckman expanded-scale *p*H meter. Samples of water for phytoplankton identification were preserved using a modified Lugol's solution described by Verduin (1960). Membrane filter techniques were used to make rough quantitative estimates.

DESCRIPTION OF THE LAKE

Located in the Tanana Valley in interior Alaska, at a latitude of 64°52″N and 146°52″W, Smith Lake has a surface area of somewhat less than 40 acres, a maximum depth of 3.5 m, and a mean depth of 2.0 m. It is located on a wildlife study area owned by the University of Alaska, and is therefore not subject to extensive recreational use. Some areas of the watershed are under cultivation, and it is possible that fertilization of this land may affect the nutrient content of the lake during the time of year when there is considerable runoff. The lake lies in a depression in a forested region which is dry during the summer, but is essentially a marsh during the spring-thaw period. There is no permanent inlet, but during the spring thaw, much of the water enters through two distinct streams. There is a single outlet, also functional only in the spring.

The lake water shows a strong brown color, which is characteristic of some arctic and subarctic lakes. The responsible substance in the lake appears to be similar to the yellow-brown material described by Shapiro (1964). It is very stable, not readily precipitated, and absorbs light strongly in the shorter visible wave lengths.

The climate of the region is continental subarctic with extremely cold winters and rather warm summers and an abrupt transition between the seasons, especially in spring. The period of ice-cover lasts from mid-November to the end of May, the ice thickness reaching a maximum of 1.5 m, with a snow cover up to a thickness of 0.5 m.

SEASONAL VARIATIONS IN NITROGEN UPTAKE AND PHYTOPLANKTON POPULATIONS

The first population of phytoplankton to develop in spring followed a long winter period without any evidence of such organisms in the water. This initial population accumulated under the ice, appearing initially in the "deep" water adjacent to the mud surface (2.5 m), and was first detected by rapid increases in the chlorophyll and particulate nitrogen contents of the water in May (Fig. 1). The nitrogen uptake experiments showed that this population predominantly used ammonia for a nitrogen source, with some detectable nitrate uptake (Fig. 2). The organisms present were dominated by micro-flagellates. *Euglena*, *Chlamydomonas*, *Mellamonas*, and *Chlorella* were among the positively identified forms. Most of the smaller cells were not identified. The rate of ammonia removal at the peak of this growth was 13 μg liter^{-1} hr^{-1}. The amount of ammonia available in the water at the beginning of the bloom was 100.53 μg liter^{-1}. Ultimately, both the standing concentration of ammonia in the water and the ammonia uptake rate declined until no ammonia remained in the water. An excess of 133 μg liter^{-1} day^{-1} of ammonia was used over the amount apparently available, and the peak of the bloom coincided with the time when most of the ammonia had moved

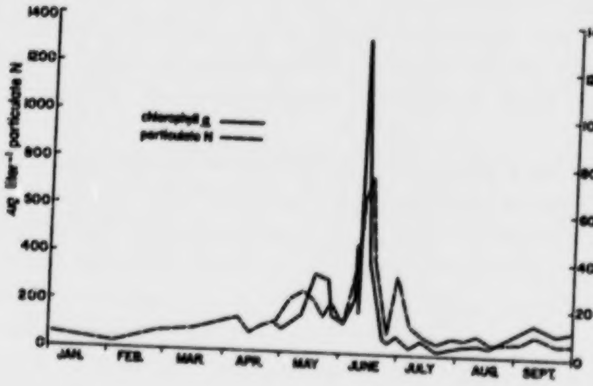

FIG. 1. Chlorophyll *a* and particulate nitrogen concentrations, Smith Lake surface water, 1964.

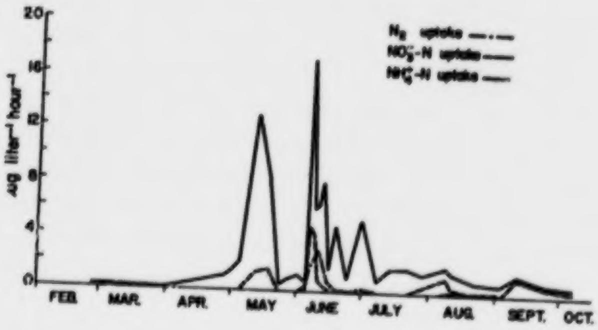

FIG. 2. Uptake rates for three inorganic nitrogen sources, Smith Lake surface water, 1964.

into the particulate fraction. Concentrations of ammonia in the water during this bloom and the succeeding population peaks were:

Date:	April 14	May 13	May 23	May 27	June 8	June 10	June 25	July 13
Concentration (μg liter^{-1})	449.96	100.52	43.82	0.00	9.10	30.10	230.58	80.78

In 1964, the ammonia content of the runoff water which entered the lake through the temporary inlet ranged from 112.7 μg liter^{-1} on May 5 to 92.2 μg liter^{-1} on May 18. By May 27, it had declined to 27.6 μg liter^{-1}. Although this was an additional source of ammonia for the under-ice population, there was only a small volume of water entering the lake during the early part of May. By the end of May, when inflow increased, the ammonia content of this became low, and this source seemed unlikely to compete in importance as an additional nitrogen source with biological regeneration of ammonia within the lake itself.

In June, a spectacular bloom of *Anabena flos-aquae* followed the melting of the ice, and occurred during the period of rapid warming and increase in day length which culminated in a daylight period of approximately 24 hr on June 21. This population was concentrated near the surface. At this time, both the particulate nitrogen and the chlorophyll contents of the water reached their maximum peaks for the year (Fig. 1). This *Anabaena* population accounted for almost all the nitrogen fixation which took place during the year in this lake. The particulate nitrogen content (a useful approximation of the cell nitrogen content) and the nitrogen fixation rate increased simultaneously. The particulate nitrogen peak corresponded with the peak in the almost unialgal population of *Anabaena*, which was associated with nitrogen fixation rates (Fig. 3) approaching 1 μg liter^{-1} hr^{-1}. In spite of this nitrogen fixation, ammonia remained quantitatively many times more important as a nitrogen source and the uptake of nitrate also exceeded the uptake of molecular nitrogen (Fig. 2). There was very little ammonia present at the beginning of the *Anabaena* bloom. Most of the nitrogen was probably being released from the organic nitrogen fractions, both dissolved and particulate, with some cycling of newly assimilated and newly fixed nitrogen.

The cause of the abrupt termination of the bloom, even more extreme in 1964 than in 1963, is unclear. A spectacular increase in *p*H from the normal 7 to a value above 10 preceded the decline in both years, followed by restoration of normal *p*H within a day or two. This increase was probably caused by the extremely high photosynthetic rates during this time. The algae started to clump and form akinetes, and then disintegrated within a day or two. There may have been a relationship between bloom decline and *p*H increase; several mechanisms are possible. Nitrogen fixation requires a rather high supply of trace metals which are not essential or are needed in smaller amounts for growth on other nitrogen sources. Among these are molybdenum and iron.

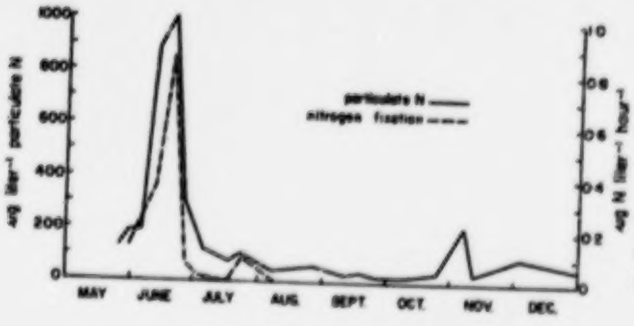

FIG. 3. Particulate nitrogen concentrations and nitrogen fixation rates in Smith Lake surfaces water, 1963.

In waters containing a high complement of colored material, the availability of iron has been shown to decrease with an increase in *p*H (Shapiro, 1964). The reduced availability of copper even at normal *p*H values was mentioned in the methods discussion above, and therefore it seems possible that this may have been an effective mechanism. Although an inadequate supply of CO_2 at high *p*H values could easily have limited the rate of photosynthesis, it seems less likely to have caused abrupt termination of a bloom. However, the response to any environmental deficiency may be the production of akinetes and the initiation of a dormant stage. The autotoxicity or autoinhibition of a dense population of blue-green algae can not be discounted, but there is insufficient information on the possibilities of such a mechanism.

During the remainder of the summer, ammonia remained the most significant source of nitrogen, with a relatively constant low concentration of this nutrient in the water, and relatively low uptake rates. Several minor populations of phytoplankton were found during this period, with *Aphanizomenon* predominant during much of the summer. A few *Anabeana* filaments were found and *Selenastrum* was another frequently found form. Zooplankton increased both in size and number during the summer, and grazing probably controlled the production of phytoplankton during July and August. In the fall, a brief pulse of algae, dominated by *Gymnodinium*, was found. During this period, nitrate uptake became quantitatively equal to ammonia uptake. This fall bloom was of minor significance compared with either of the spring pulses.

FACTORS CONTRIBUTING TO THE AVAILABILITY OF NITROGEN SOURCES

Events under the ice during the winter appeared to be important in determining the forms of nitrogen available to the phytoplankton in the spring. During the fall, the ammonia content of the water increased, accompanied by a similar increase in the nitrate concentration (Fig. 4). This was certainly due to the regeneration of ammonia from the organic nitrogen fractions, and its subsequent oxidation to nitrate by the bacterial process of nitrification. However, by early spring, the oxygen content of the water began to decline, ultimately resulting in anoxic conditions under the ice cover.

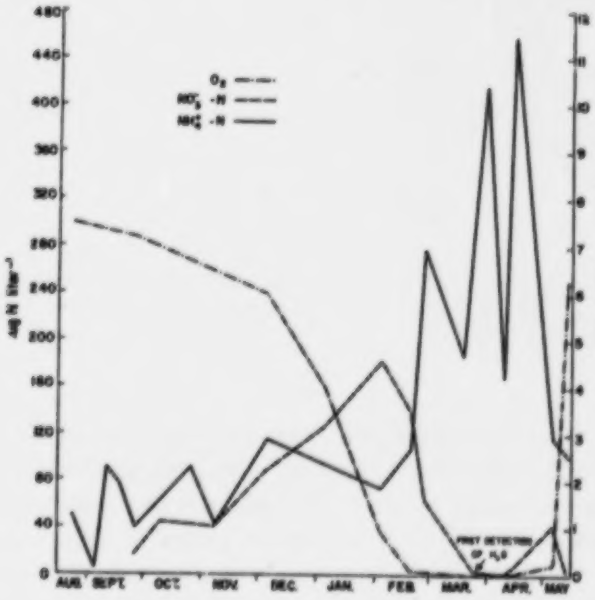

FIG. 4. Ammonia, nitrate, and dissolved oxygen concentrations in Smith Lake water under the ice, 1963–64.

As the oxygen content reached a low level, nitrate began to decrease in concentration until it disappeared completely. Hydrogen sulfide appeared in the water (detectable by odor) after the nitrate became exhausted.

The disappearance of nitrate can be attributed to dentrification, the bacterial dissimilatory reduction of nitrate, for the following reason. The reduction in nitrate concentration was occurring at a time when the oxygen content of the water was very low, and it is under these conditions that nitrate is used as a hydrogen acceptor by microorganisms, and reduced to nitrogen gas. ^{15}N tracer measurements have confirmed such reduction of nitrate to nitrogen gas in Smith Lake water at a rate adequate to account for the observed loss (Goering and Dugdale, 1966). As the nitrate concentration became low, sulfate took over a similar role, resulting in the accumulation of hydrogen sulfide.

Assuming that all the nitrate lost was denitrified, we can estimate a rate of dentrification in the water during this anoxic time from the rate of decrease in its nitrate content. If the vertical distribution of nitrate is plotted (for several dates) during this time (Fig. 5), the areas between the depth distribution lines represent the nitrate content for the water column, and, after integration of these areas, rates of nitrate loss can be determined from the differences.

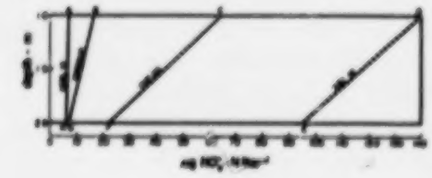

FIG. 5. Vertical distributions of nitrate in Smith Lake water, spring, 1964.

The total amount of nitrate lost during the spring amounted to 106.4 μg liter^{-1}, of which 74.2 μg liter^{-1} was lost during the first anoxic week.

Ammonia continued to increase in concentration in the water during this entire spring period. A high ammonia content was thus available to the phytoplankton in the spring, but very little nitrate.

GENERAL DISCUSSION

This seasonal work on nitrogen uptake in Smith Lake strongly supports the observation on Sanctuary Lake that ammonia is used by the population as a whole simultaneously with nitrogen supplied by nitrogen fixation (Dugdale and Dugdale, 1965). The proportions of ammonia, nitrate, and molecular nitrogen used in June were very similar in Sanctuary Lake to those shown for Smith Lake in Fig. 2. These conclusions can be applied only to the whole system, since no information obtained by the methods used applied to specific organisms within the population. However, the blue-green alga *Anabaena flosaquae* showed the most spectacular growth rate and abundance during the nitrogen-fixing phase.

The *Anabaena* bloom was observed using the methods described above during the 1963 and 1964 seasons, but was also noted during 1965, 1966, and 1967. The blooms were very similar in timing during these years.

A second conclusion, which emerges both from the information on the under-ice bloom and from the blue-green algal bloom, relates to the role of ammonia supply from other nitrogen fractions during a phytoplankton pulse. During both production periods, the amount of ammonia used was considerably in excess of the amount apparently available in the water. The ammonia content of the water actually increased during the *Anabaena* bloom. A steady rate of supply from the organic fraction is implied, and the appearance of ammonia in the water after the decline of the June bloom confirms this. The standing amount of ammonia in the water is, of course, determined by the difference between the rates of supply and removal. The significance of the instantaneous ammonia content in the water is thus of limited value in determining the nutrient available, unless the turnover rate of such ammonia is also known. Evidence supporting high ammonia turnover rates during algal blooms is presented in Billaud (1967). A very high concentration of ammonia, as found in the water prior to the under-ice bloom in May, however, suggests the potential for production.

The reappearance of oxygen in the water after the spring anoxic period coincided with the May algal production, and these organisms may have been responsible for producing the oxygen photosynthetically. By this time, there was considerable light, and penetration through the ice and snow could have been adequate. There was no evidence of algal production during the dark season, and therefore, no apparent need to postulate any important role for heterotrophy in the development of the under-ice bloom.

ACKNOWLEDGMENTS

This study was supported in part by the National Institutes of Health grants WP-00422-02, WP-00422-03.

The technical assistance of Robert Clasby, William Zoller, and Judith Thompson is acknowledged with appreciation. This work could not have been carried out without the support of Dr K. M. Rae.

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NITROGEN FIXATION IN ICE-COVERED ARCTIC AND SUBARCTIC LAKES[1]

V. Alexander

[1] I wish to acknowledge the valuable assistance rendered by Mr. D. M. Schell in connection with the gas chromatography and of Mrs. Rose Marie Nauman in assisting with the subarctic experiments. Dr. Rita Horner kindly supplied the information on the ice organisms in Nuwuk Lake.

INTRODUCTION

The measurement of nitrogen fixation in natural waters recently received a great stimulus through the introduction of the acetylene reduction technique by Stewart, *et al.* (1967). This method of estimation depends on the reduction of acetylene to ethylene by the nitrogen fixing enzyme. The high sensitivity and also the simplicity of the technique render it extremely valuable for field assays. However, there have been some problems in connection with its application which have frequently precluded optimal results. Some of these, we had not solved during the first season of such measurements, so that the results are not quantitative. During the terminal portion of this program, while planning nitrogen fixation work in connection with the Tundra Biome Program for I.B.P., many of these problems were solved.

Now that we know that nitrogen fixing blooms play an important role in subarctic lakes during the early summer, we were interested in finding out more about the role of nitrogen fixation during the ice-covered portion of the year, and in assaying as wide a variety of microenvironments as possible. Arctic lakes under ice-covered conditions had not hitherto been studied in respect to nitrogen fixation, although in Antarctica nitrogen fixation by blue-green algae has been found significant (Holm-Hansen, 1963; Fogg and Stewart, 1968).

The work described here includes preliminary experiments which were carried out on lakes in the Tanana Valley of central Alaska, with the aim of determining whether nitrogen fixation occurred under anoxic conditions in these lakes, and also to find out whether nitrogen fixation was a property of the extensive *Aphanizomenon* blooms which are found in many of these lakes during the mid-summer period. During a ten day visit at the Naval Arctic Research Laboratory in Barrow during June, 1969, a series of lakes were assayed for nitrogen fixation. The lake waters, the flora at the ice-mud interface in lakes which were frozen to the bottom, and organisms found within the ice were included.

METHODS

In order to measure nitrogen fixation, a sample was placed in a 20 cc vial equipped with a septum. A mixture of helium, oxygen and carbon dioxide was introduced through a 20 gauge hypodermic needle, and the air swept out through a second needle for a vent until the contents were free of elemental nitrogen. In the case of anoxic waters, helium alone was used. Both needles were withdrawn and then about 2 cc of pure acetylene were injected. The sample was allowed to incubate for one or more hours, and then tested for the presence of ethylene. If testing was not carried out immediately, the samples were preserved with 50% trichloroacetic acid.

The analysis of the head gas over the samples was carried out on a Varian model 1520 gas chromatograph equipped with a flame-ionization detector. A 100 μl sample of head gas was used, which is adequate for positive estimation of ethylene reduction if 0.1% of the injected acetylene is reduced. This corresponds to 3×10^{-9} g of ethylene.

Standard mixtures of acetylene, methane and ethylene were used for calibration of the hydrocarbon peaks. A 6 foot 1/8" diameter stainless steel column containing 60-80 mesh Poropak R gave excellent separation of CH_4, C_2H_2 and C_2H_4 at 60°C. Blank samples into which no acetylene had been added, or samples poisoned with trichloroacetic acid prior to addition of acetylene were used to guard against possible erroneous results due to indigenous sources of ethylene production or abiotic reduction of acetylene.

EXPERIMENTS AND RESULTS

Smith Lake, May 23, 1969

The lake was still ice-covered at this time, but oxygen was present. Four aliquots of lake water, and in addition one treated with trichloroacetic acid were treated with acetylene as described above. An additional sample was merely flushed with the gases, and no acetylene was added. Incubation was for 3 hours 20 minutes. All assays for ethylene production were negative.

Ace Lake, June 4, 1969

Ace Lake does not mix in the spring, and anoxic water is present below 3 meters. This experiment was run to find out whether nitrogen fixation was taking place under anoxic conditions. Duplicate samples from 0 and 4 meters were tested. The 4 meter sample was flushed with helium alone. A control from each depth was innoculated with trichloroacetic acid prior to the addition of acetylene. All samples were incubated *in situ* for one hour, and then poisoned with 0.5 ml of 50% trichloroacetic acid. No ethylene production was detected.

Ace Lake, August 28, 1969

This experiment was carried out at a time when a large number of *Aphanizomenon* sp. were present. The results, shown in Table 1, show that there appeared to have been some acetylene reduction, but at an extremely slow rate. An hour is usually ample to positively detect nitrogen fixation. In this case it took 18 hours. However, the fixation did appear to be light-dependent. In addition to the *Aphanizomenon* a smaller number of *Anabaena* sp. filaments with heterocysts were observed in the population. These may have been responsible for the nitrogen fixation, since if the numerous *Aphanizomenon* had been actively fixing, the rates should have been much higher.

Barrow Area Experiments

The results of the Barrow experiments are shown in Table 2. In Imikpuk Lake, adjacent to the laboratory, nitrogen fixation was detected in the water under the ice, but not in the mud samples, and an isolated filament of a blue-green algae yielded negative results. In Nuwuk Lake, a saline lake, nitrogen fixation was again detected in the water below the ice, but not in the deeper water, nor in the algae populations found in the ice. Sewage Pond, a small polluted pond which was frozen to the bottom, did not fix nitrogen. No fixation was detected in a large lake immediately to the West of Lake Teshekpuk, which was designated Sta. #1 in the table. Loon Lake, adjacent to Ikroavik Lake, also yielded negative results for the ice algae and algae of the ice-mud interface.

CONCLUSIONS

The results of the experiments carried out here suggest that nitrogen fixation is not a property of the ice-mud interface or of the populations within the ice in frozen arctic lakes, but that it does take place in the water immediately under the ice cover. Since dark and light samples were not run, we cannot tell whether photosynthetic organisms are involved. Although counts were not made, blue-green algae appeared to form a considerable proportion of the population in Imikpuk Lake. This was not true, however, of Nuwuk Lake. Obviously a more detailed survey of the organisms present in connection with future assays will be needed. The few experiments in the subarctic have confirmed the fact that nitrogen fixation in significant amounts is important only in connection with blooms of *Anabaena* sp., since the rates observed in connection with the *Aphanizomenon* were so extremely low.

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Table 1. Results of Acetylene Reduction Nitrogen Fixation Experiment.

Ace Lake, August 28, 1969

Sample	Incubation Time	Presence of Ethylene
Control	4.5 hours	-
Surface water	4.5 hours (dark)	-
Surface water	4.5 hours	?
Surface water	18 hours	+
Surface water	18 hours (dark)	-

Incubations at 20°C and 100 foot-candles Gro-lux light.

Table 2. Results of Nitrogen Fixation Assay Using Acetylene Reduction.

Barrow, Alaska - June 1969

Sample	Incubation Time (h)	Presence of Ethylene	Comments
Imikpuk Lake			
Lake water	3.25	+	
Control	3.25	-	
Water + mud	3.25	-	methane present
Mud-water conc.	3.25	-	methane present
Blue-green filament	3.25	-	trace of methane
Nuwuk Lake			
Lake water	4.0	+	*Nitzschia frigida* colorless flagellates Dinoflagellate
Control	4.0	-	
4 meter water	4.0	-	
Ice algae	4.0	-	*Chaetoceros ceratosporum* *Fragilariopsis* sp. *Nitzschia frigida* - dominant colorless flagellates - 4-24μ unidentified dinoflagellates some bacteria
Sewage Pond			
Algae from mud-ice interface	4.0	-	
Station #1			
Middle section of ice core	3.0	-	
Section of core between middle and bottom	3.0	-	
Bottom section of ice core	3.0	-	
Loon Lake			
Ice core algae	3.0	-	
Algae mat from ice-mud interface	3.0	-	green algae, both straight and branched filaments

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IMPROVED INCUBATION AND GAS SAMPLING TECHNIQUES FOR NITROGEN FIXATION STUDIES

By

Donald M. Schell and Vera Alexander

The measurement of nitrogen fixation in natural waters recently received a great stimulus through the introduction of the acetylene reduction technique by Stewart, *et al.* (1967). This method of estimation depends on the reduction of acetylene to ethylene by the nitrogen fixing enzyme. The high sensitivity and also the simplicity of the technique render it extremely valuable for field assays. However, there have been some problems connected with its application which have frequently precluded optimal results. Perhaps the most serious difficulty has been the use of an agent to terminate biological activity at the end of the chosen incubation period. Under field conditions, there is an inevitable time lag between the termination of the experiment and gas chromatography of the gas phase for ethylene assay. None of the metabolic poisons hitherto used have been satisfactory and frequently the results of gas analysis following the use of trichloroacetic acid, Lugol's solution or sulfuric acid have been unsatisfactory. The only satisfactory method has been to immediately remove the gas sample into a syringe and to cap the syringe. This is not a good way of storing samples during an extended time lapse, and the amount of gas sample available is limited.

Faced with running numerous nitrogen fixation determinations both in the alpine tundra of the Alaska Range and on the Arctic Slope tundra, the storage problem of gas samples over several weeks posed a serious impediment. We solved this by using B-D Vacutainers® manufactured by Becton-Dickinson Co. We used these in conjunction with two different types of incubation containers, one for phytoplankton samples (aqueous) and one for emergent plants. Aqueous samples were incubated in 25 cc vials fitted with septa as has been described (Stewart, *et al.* 1967). Macrophytic samples were incubated in heavy plastic bags which were secured to collared glass tubes, also fitted with septa. After assembly, the included air was withdrawn from the bag through a hypodermic needle connected to a vacuum source and, after flushing with an incubation mixture of $Ar\text{-}O_2\text{-}CO_2$, the volume surrounding the plant was reduced to near minimum by again applying suction through the septum, collapsing the bag around the plant. The acetylene was then injected. By virtue of the minimum volume, the appearance of ethylene through reduction of the acetylene was enhanced. This technique is also ideal for use on terrestrial samples, such as lichens and small plants.

After incubation, gas samples were taken from the incubation vessels into Vacutainers. The latter are pre-evacuated glass tubes fitted with heavy septa (Figure 1, A). A double-ended hypodermic needle (B) was attached to a plastic sleeve as shown in the illustration (C). The Vacutainer tube was inserted into this sleeve such that the needle penetrated into but did not pass through the heavy septum (D). Then the other end of the needle was inserted into the incubation vessel, and by applying a little pressure, the needle into the Vacutainer was pushed through the septum, allowing the gas sample to enter the tube. Removal of the Vacutainer tube from the syringe sealed the sample until ready for chromatography. No ethylene or other hydrocarbon was detected in unused unsterile Vacutainers, although the sterilized Vacutainers did contain traces of methane and ethylene. Use of the presterilized Vacutainers is therefore undesirable, although it was found that the ethylene content was sufficiently small and uniform that corrections could be applied if it was necessary to use them. No deterioration of the samples through loss or contamination was apparent in any of the 500 or so samples run over a thirty day period.

An additional advantage over poisoning the sample in the incubation vessel is the possibility of immediate recovery and drying of the biological specimen for subsequent dry weight or nitrogen determination. Finally, the same setup proved ideal for corroboration experiments using $^{15}N_2$ gas instead of acetylene, and Vacutainers may be used to collect gas samples for exact determination of the isotope ratio of the gas supplied in the reaction vessel.

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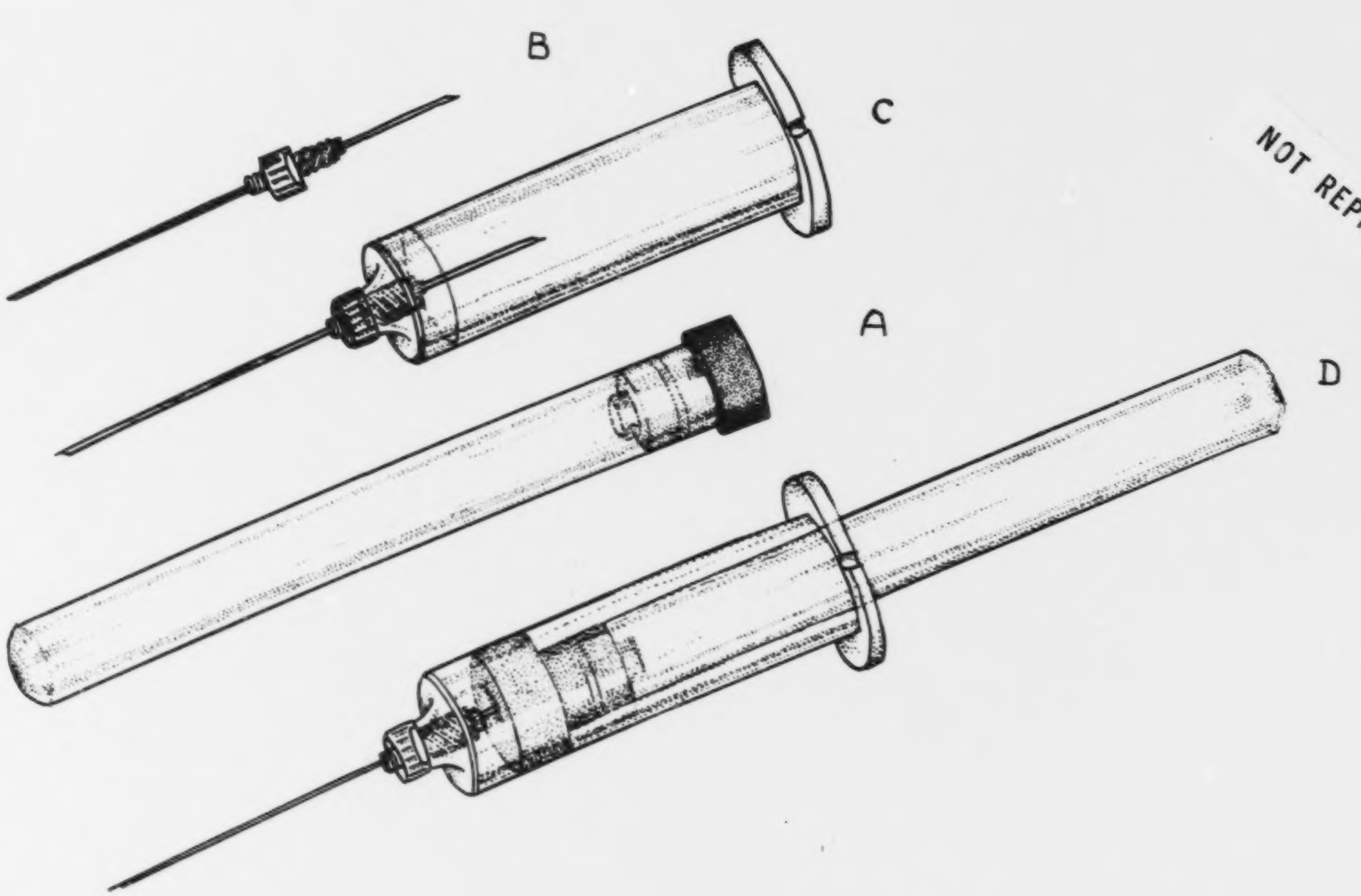

Fig. 1. Illustration of B-D Vacutainer.

SECTION TWO

AMMONIA SUPPLY AND TURNOVER

RELATIONSHIPS BETWEEN TURNOVER RATES IN THE BIOLOGICAL NITROGEN CYCLE AND ALGAL PRODUCTIVITY

By

V. Alexander

ABSTRACT

Rates of ammonia supply were measured using a ^{15}N isotope dilution technique, and simultaneous determinations of the uptake rates of ammonia and nitrate were included. The results are presented in conjunction with primary productivity values. Turnover times of less than one day were found for the dissolved ammonia fraction during the summer months in moderately productive subarctic lakes.

INTRODUCTION

The problem of accelerated eutrophication is concerning people throughout large portions of the world. The principle causative factor is the increased release of nutrient compounds into natural waters. Fundamental information is needed to evaluate the effects of such additions on the biological behaviour of aquatic systems. Although the total biomass of organisms which can be produced within a discrete environment is a function of the total amount of nitrogen and phosphorus available, without knowing the details of the cycling behaviour of these elements, it is difficult in practice to correlate nutrient input with biological availability. Baalsrud (1967) discussed the role of nutrient input in increasing marine productivity, and in summing up the published work points out that in the case of phosphorus the lack of a clear correlation is due to the ability of the plants to indulge in "luxury" consumption, to their ability to vary their cell phosphorus content within wide limits, and also to the rapid turnover rate of the phosphorus within the aquatic system. Information on the behaviour of nitrogen is sparse. Dugdale (1969) gives an estimate for ammonia turnover in tropical marine surface waters on the order of 40 hours. Previous work in our laboratory on freshwater systems has indicated a much more rapid turnover (Billaud, 1967).

This paper will deal with a study of the turnover rates of inorganic nitrogen compounds in freshwater, with emphasis on the role of ammonia. Ammonia was found the most rapidly used nitrogen source in freshwater lakes (Dugdale and Dugdale, 1965; Billaud, 1968). The uptake rates as measured by ^{15}N tracer experiments were considerably in excess of those expected on the basis of the ammonia concentrations present in the water (Dugdale, 1965). This suggests a rapid turnover for ammonia, especially during periods of high phytoplankton productivity. Ammonia, during a period of time when it was being used exclusively in Smith Lake, a small subarctic lake, remained low in concentration with only minor fluctuations. Nitrification was apparently not an important process during this time, since nitrate, too, remained at a rather constant low level, and in the absence of removal by uptake, nitrification would have resulted in an increase in concentration.

It seems reasonable to assume, then, that nitrification cannot compete with the uptake of the available ammonia by phytoplankton accompanying high productivity, and that the ammonia is being recycled rapidly. In Fig. 1, a simplified version of the nitrogen cycle, this implies that only the bottom three compartments are active, and that the ammonia is being transformed rapidly between these. According to this scheme, nitrification can be expected to become important only when the demand for ammonia by the phytoplankton becomes minimal, and the residence time for ammonia in the water is extended. The purpose of the research described here was to obtain quantitative estimates of the turnover rates for ammonia.

METHODS

The measurements of ammonia turnover in the lake waters were carried out using an ^{15}N isotope dilution technique. Labeled ammonia was added to a sample of lake water, the system was thoroughly equilibrated and immediately an aliquot was removed and the isotope ratio of the ammonia fraction was determined. Subsequently, aliquots were removed at regular time intervals and the ammonia nitrogen isotope ratio was determined for each. The results gave a rate of dilution of the added labeled ammonia by unlabeled ammonia from other nitrogen fractions in the water, from which the ammonia supply rate was calculated.

In order to determine the isotope ratios, the ammonia was collected from the aliquots by distillation in a vacuum still. The still design is shown in Figure 2. A pressure-vacuum pump was used to maintain a moderate vacuum, the sample was placed in the glass flask which is heated by a mantle. MgO was added to raise the pH of the sample. Air, passed through acid and base solutions, swept through the system in a very slow stream to aid in carrying the distillate into the condenser to be collected in 50 ml of .1 N HCl. The HCl containing the ammonia sample was boiled down to a few ml volume and the ammonia was converted to N_2 using alkaline hyprobromite. The conversion was carried out in a high vacuum system, and the evolved nitrogen was to be pumped in a Bendix model 17-210 Time of Flight mass spectrometer for isotope ratio determination. Experiments using this method on lake waters showed good reproducibility in aliquots removed from the incubation vessel at short successive time intervals, with the exception that any samples which became dry during the boiling down process had a significantly lowered $^{15}N/^{14}N$ isotope ratio.

Turnover times for the dissolved ammonia in the lake water were calculated using the formula:

$$\underset{\text{(days)}}{\text{Turnover time}} = \frac{NH_4^+ \text{ - N present } (\mu\text{g-at liter}^{-1})}{NH_4^+ \text{ - N supply rate } (\mu\text{g-at liter}^{-1}\ \text{day}^{-1})}$$

Ammonia and nitrate uptake were measured using the methods described in Dugdale and Dugdale (1965). Incubation with ^{15}N labeled ammonia and nitrate was carried out *in situ*, and following incubation the particulate material was recovered on a glass micropore filter, and converted to N_2 using the Dumas method of Barsdate and Dugdale (1965).

Chlorophyll *a*, determined on 90% acetone extracts of phytoplankton recovered on a glass filter, was used as the main indicator of phytoplankton biomass. Primary productivity was measured using the ^{14}C method of Steeman Nielson (1952) using *in situ* incubation, and particulate nitrogen (PN) determinations employed a Coleman nitrogen analyzer, also using glass filter-collected particulate material. Ammonia determination used the method of Richards and Kletsch (1964), and nitrate was done by the method given in Strickland and Parsons (1960), with minor modifications to adapt the method for use in the highly-colored lake waters encountered in this work.

RESULTS

Smith Lake, a small subarctic lake near the University of Alaska, had been studied over a period of several years both in terms of its general limnology and of its nitrogen cycle. The occurrence of an annual blue-green algal bloom in June has made it possible to make detailed observations on the behaviour of nitrogen cycle transformations during such a bloom. Initial measurements of ammonia turnover rates had indicated a maximum in ammonia supply following the peak of the bloom although no measurements had been made during the bloom. In the present study, ammonia and nitrate uptake, ammonia supply, primary productivity and chlorophyll *a* determinations were made at two day intervals prior to and during the bloom. The results of the nitrogen uptake determinations are shown in Table 1. These results indicate that during the blue-green algal bloom, turnover times for the ammonia fraction ranged from 0.12 to 0.62 days, with a tendency for shorter times to occur with increased primary productivity rates and ammonia uptake rates. However, the shortest turnover time occured prior to the bloom, probably as a result of ammonia regeneration following an earlier spring under-ice period of high productivity: thus the Smith Lake ammonia turnover time was less than one day at all times, and frequently only a small fraction of a day.

Similar determinations were made on a second lake in the same area. Ace Lake, with a smaller connected lake named Deuce Lake, comprises a pair of interesting lakes since they tend to mix only partially and have permanently anoxic subsurface waters. The water, in common with Smith Lake, is highly colored. Ace Lake does not tend to produce striking blooms, although during much of the summer a considerable population of *Aphanizomenon* sp. exists in the euphotic zone, and a second population, unidentified yet, is found at the boundary region of anoxic water, where the light intensity is usually less than 1% of the surface. The uptake experiments showed that here, too, ammonia uptake is more important than nitrate uptake, and rates of ammonia uptake approaching half the peak Smith Lake values were observed (Table 3). The primary productivity rates in the surface waters confirm the trend of the ammonia uptake results. Maximum ammonia supply was measured following the maximum in primary productivity, but in connection with the peak in particulate nitrogen. Turnover times here were less than a day during the summer, although by the early fall they had extended to approximately a day, (Table 4), with a range between 0.84 and 1.23 days, with the exception of one occasion with only 0.03 days following the productivity maximum.

DISCUSSION

Ammonia turnover times as calculated here are only valid if no appreciable change in ammonia concentration is occurring. This is not true of the fall period in these lakes, but is a reasonable assumption during the summer months. The results obtained indicate turnover times of less than one day at all times, with rapid release of ammonia following the production of large amounts of particulate nitrogen, and also rapid turnover during the summer in moderately productive lakes.

The increase in ammonia supply rates during and again following phytoplankton blooms may be explained by microbiotic cycles of the type described by Silvey and Roach (1964), and also by the excretion of ammonia by the algae themselves or by zooplankton grazing on the algae. Blue-green algae tend to excrete ammonia, especially nitrogen-fixing forms (Fogg, 1952). The Smith Lake bloom is almost totally composed of *Anabaena flos-aquae*, and depends on nitrogen fixation for a large portion of its nitrogen supply (Billaud, 1968). Excretion of newly-fixed nitrogen as ammonia almost certainly plays a role.

The ammonia supply rates imply also that substantial regeneration of inorganic nitrogen from the particulate and dissolved organic fractions takes place in the surface waters of lakes. No consideration of input and output of ammonia through water-movements or from the sediments has been included here. The rate of ammonia production within the system is of the same order of magnitude as uptake by organisms during the summer productive season, and thus is a sufficient explanation of the ammonia source in the lake waters studied. While not intending to discount the importance of sediments in nutrient generation, their significance may be greater as an annual basis in the regeneration of ammonia and also nitrification, whereas during this productive season local regeneration within the euphotic zone may be more important.

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TABLE 1 Uptake of Inorganic Nitrogen Compounds in Smith Lake Surface Water, 1968

(Rates in μg-at Liter^{-1} Hr^{-1}, Concentrations in μg-at Liter^{-1})

		NH_4^+-N		NO_3^--N	
Date	PN	Uptake	Conc.	Uptake	Conc.
May 21	1.42	.01	2.75	.012	0.4
May 28	7.47	.10	0.71	.02	0.4
May 31	[10.00]	.16	[1.00]	.19	---
June 5	13.69	.23	2.81	.12	0.4
June 7	[15.00]	.25	[2.00]	.03	---
June 10	28.38	.36	2.35	.03	---
June 12	28.38	.80	1.35	.07	0.1
June 14	[28.38]	.29	[1.35]	.25	---
June 17	17.19	---	---	.59	---

TABLE 2 Ammonia Supply, Turnover and Primary Productivity, Smith Lake Surface Water, 1968

Date	Chlorophyll a (μg Liter^{-1})	Photosynthetic Carbon Uptake (μg C Liter^{-1} Hr^{-1})	NH_4^+-N Supply (μg-at Liter^{-1} Day^{-1})	NH_4^+-N Concentration (μg-at Liter^{-1})	Turnover Time For NH_4^+-N (Days)
May 21	16.4	21.03	97.42	2.75	0.03
May 29	11.9	27.60	5.83	0.71	0.12
May 31	14.9	35.74	2.29	[1.00]	0.43
June 5	17.1	46.74	4.54	2.81	0.62
June 7	68.5	---	7.15	[2.00]	0.28
June 10	16.4	35.95	---	---	---
June 12	32.6	168.67	8.91	1.35	0.15
June 14	47.7	11.07	8.67	[1.35]	0.16
June 17	12.8	17.55	8.01	---	---

TABLE 3 Uptake of Inorganic Nitrogen Sources in Ace Lake Water, 1968

(Rates in µg-at Liter^{-1} Hr^{-1}, Concentrations in µg-at Liter^{-1})

Date	PN	NH_4^+-N		NO_3^--N	
		Uptake	Conc.	Uptake	Conc.
May 24	13.03	0.03	12.50	0.00	2.1
May 29	40.65	0.63	4.50	0.24	0.6
June 6	5.94	0.06	2.10	0.01	0.6
June 13 (0m)	4.97	0.11	2.30	0.01	0.3
June 13 (1m)	6.41	0.01	2.35	0.12	0.0
June 20	6.41	0.29	0.81	0.00	0.7
June 27	15.23	0.26	3.97	0.02	0.4
July 5	36.88	0.29	3.57	0.25	0.6
July 11	7.39	0.09	3.11	0.01	0.4
July 18	3.36	0.04	4.42	0.00	0.5
July 23	4.78	---	0.66	0.00	0.5
Aug 1	6.37	0.04	1.70	0.00	0.5
Aug 8	2.39	0.02	2.70	0.00	0.9
Aug 15	2.20	---	2.80	---	0.3
Aug 23	3.30	0.03	2.30	0.01	1.8
Aug 29	12.37	0.06	2.40	0.01	0.4
Sept 5	4.27	0.01	3.50	---	0.4
Sept 21	6.95	0.02	5.60	0.00	1.0
Oct 8	9.45	0.01	9.45	0.01	2.2

TABLE 4 Ammonia Supply and Primary Productivity

Ace Lake, 1968

Date	PN μg Liter^{-1} Hr^{-1}	Productivity μg C Liter^{-1} Hr^{-1}	NH_4^+-N Supply μg-at NH_4^+-N Liter^{-1} Day^{-1}	NH_4^+-N Concentration μg-at Liter^{-1}	Turnover Time (Days)
June 6	5.94	9.58	2.5	2.10	0.84
June 13	4.97	11.28	0	2.30	---
June 20	6.41	43.87	3.0	0.81	0.27
July 5	36.88	18.52	115.8	3.57	0.03
Aug 13	2.20	0.88	2.71	2.8	1.03
Sept 3	4.27	---	2.85	3.5	1.23
Oct 8	9.65	8.32	0	10.6	---

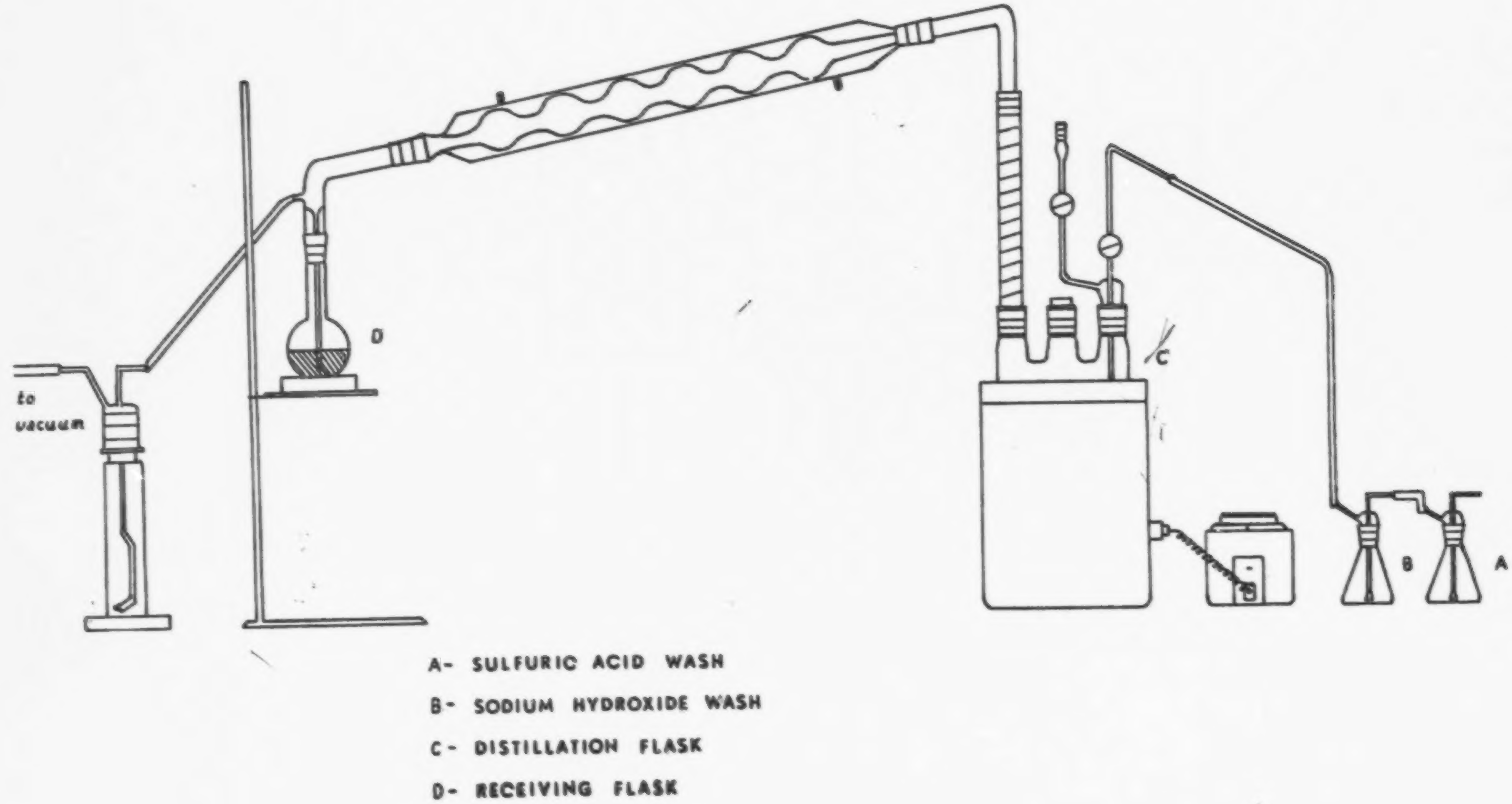
to vacuum
D
C
B
A
A- SULFURIC ACID WASH
B- SODIUM HYDROXIDE WASH
C- DISTILLATION FLASK
D- RECEIVING FLASK

Fig. 1. A simplified illustration of the biological nitrogen cycle.

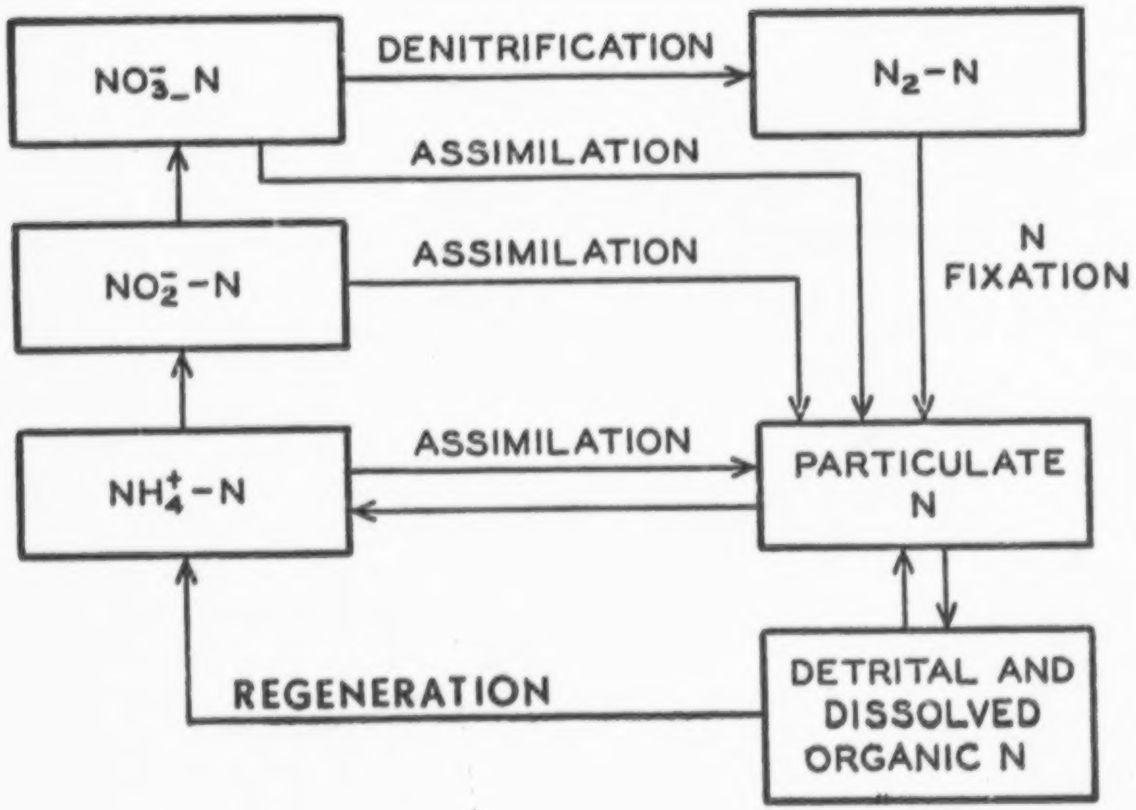
NO_3^--N
DENITRIFICATION
N_2-N
ASSIMILATION
NO_2^--N
ASSIMILATION
N FIXATION
NH_4^+-N
ASSIMILATION
PARTICULATE N
REGENERATION
DETRITAL AND DISSOLVED ORGANIC N

Fig. 2. A diagrammatic illustration of the vacuum distilllation equipment.

SECTION THREE

DENITRIFICATION AND LAKE GAS STUDIES

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RATES OF DENITRIFICATION IN THE ANOXIC ZONE OF A SUBARCTIC LAKE

By

R. C. Clasby and Vera Alexander

INTRODUCTION

Denitrification is the dissimilative reduction of NO_3 to N_2 by bacteria which use the NO_3 as a terminal electron acceptor in the place of O_2 during the oxidation of organic matter. The measurement of the rates of denitrification is a necessary step in assessing the nitrogen budget of a system. Recent estimates of these rates in the sea (Goering and Dugdale, 1966a; Goering and Cline, 1970; Goering and Pamatmat, 1970) and in lakes (Goering and Dugdale, 1966; Brezonik and Lee, 1968) have shown that denitrification may play a very important role in the nitrogen budget of certain aquatic systems. During denitrification inorganic nitrogen as nitrate is lost from the nutrient pool and therefore the process can be considered as a nitrogen sink. It has recently been proposed that denitrification may be an important nitrogen sink in the ocean (Goering, *et al.*, 1970) and in certain lakes (Goering and Dugdale, 1966b).

During our study of the nitrogen cycle in subarctic lakes we decided to determine if denitrification did occur and at what rates in a nearby lake that is in some respects quite dissimilar from the one studied by Goering and Dugdale (1966b). The lake chosen for the study was Ace Lake located near the campus. Although Ace Lake has not been studied as extensively as Smith Lake some productivity and nutrient chemistry has been performed (Billaud, 1967; Alexander and Barsdate, unpublished manuscript). Ace Lake is atypical of most lakes in the region in that spring circulation is confined to the surface and fall circulation is strongly attenuated near the bottom. Oxygen tends to be depleted below the surface during the entire year and hydrogen sulfide is evident in the anoxic layer, indicative of sulfate reduction. Nutrient levels are higher than those normally found in other lakes in the region, but do show some depletion during the summer. Nitrate in the deep water appears to remain at fairly constant levels during the spring and summer with a sharp increase during the fall circulation and a decrease through the winter (Table 1). Because of the anoxic conditions it was hypothesized that part of the nitrate loss may be a result of denitrification.

METHODS

The method of Goering and Dugdale (1966b) was used with some modifications. Samples for this study were collected from under the ice on 17 February 1970 from a depth of 3.5 m using a 0.5 l Frautschy bottle. The water samples were transferred to 5

300 ml BOD bottles and stoppers replaced to minimize atmospheric contamination. The bottles were returned to the laboratory and four of them were each inoculated with 83.33 μg-at of ^{15}N/l as KNO_3 (97.8 atom percent ^{15}N) under an atmosphere of CO_2. The fifth bottle was not inoculated and served as a control. The bottles were placed in a darkened box and incubated at 5°C. At the end of 3, 5, 9, and 13 days the samples were poisoned by the addition of 2 ppm by weight HgCl under an atmosphere of CO_2. The control was also poisoned on the 13th day. The samples were stored at 5°C until mass spectrographic examination.

For isotope analysis 5 ml subsamples were withdrawn from the BOD bottles using a 5 ml gas tight syringe (Hamilton model 1005) fitted with a Channey adapter. Figure 1 shows the manifold system used to strip the dissolved gases from the water sample. The manifold was flushed with CO_2 (Coleman grade), stop cock C was closed, a high vacuum drawn on the manifold, and then stop cocks A and B closed. A pressure of approximately 8 psi was placed on the gas stripper with CO_2 and the sample added through the septum at the top. Stopcock C was opened and the gases allowed to flow through the acetone-solid CO_2 bath where water vapor was removed. The gas pressure reached equilibrium in about one minute, fifteen seconds, at which time stopcock C was closed and B opened for fifteen seconds. CO_2 was frozen out in the liquid nitrogen bath. Stopcock B was then closed and A opened. The gas sample was then Toeppler pumped into a Bendix Time-of-Flight Model 17-210 mass spectrometer and mass peaks 28, 29, and 30 read.

The fraction of total nitrogen gas evolved from ^{15}N labeled NO_3 during incubation was calculated by the method of Hauck, *et al.* (1958). Their method considers the situation in which the N_2 molecules originate from more than one source (original dissolved N_2 and N_2 released from nitrate) and no common intermediate, where isotopic pooling can occur, is formed.

Nitrate was measured by the method of Strickland and Parsons (1960) as modified by Billaud (1968).

Oxygen was measured by the Alsterberg modification of the Winkler method.

RESULTS

Computation of d values using the expressions of Hauck, *et al.* (1958) indicate that N_2 was formed by the process of denitrification. The fraction of total dissolved nitrogen evolved from denitrification is plotted in Figure 2. To calculate the weight of nitrogen evolved it is necessary to know the weight of dissolved N_2 originally present in the sample. Since dissolved N_2 was not measured it was necessary to assume that the lake was saturated with respect to nitrogen. The value of 20.31 mg/l dissolved nitrogen at 5.0°C was used (Murray, *et al.*, 1969). The calculated rate of denitrification for the first 3 days was 125.12 μg/l-day of nitrogen. The rates for day 3 through day 9 and for day 9 through day 13 were 4.33 and 6.00 μg/l-day respectively. The spectrometer trace for day 5 gave a poor baseline and these results had to be discarded. Nitrate concentration at the 3.5 m level was 5.38 μg-at NO_3-N/l and dissolved oxygen was undetectable.

DISCUSSION

The maximum rate of denitrification measured in Ace Lake is an order of magnitude greater than that found in Smith Lake by Goering and Dugdale (1966b) of 15 μgN/l-day at 1.0 m. The rate is also significantly greater than those measured by Goering and Dugdale (1966a) for an island bay in the equatorial Pacific and by Brezonik and Lee (1968) for Lake Mendota. The reason for the high rate of denitrification in Ace Lake is not known and requires further investigation. Also unexplained is the sharp decrease in rate of denitrification after the 3rd day when only approximately 33% of the nitrate had been converted to N_2. Analysis of the samples at the end of the experiment showed that considerable quantities of nitrate were still present ($>$45μg-at NO_3-N/l).

Errors in the experiment would tend to give lower than actual rates. A positive error in the measurement of nitrate, which is probable in the type of water used, would decrease isotopic dilution and result in an under estimate of the rate of denitrification. The calculated rate would also be low if the amount of dissolved nitrogen gas originally present was higher than assumed from the saturation tables because the weight of N_2 evolved is a function of the original N_2 present times the factor d. If denitrification is taking place under the ice it would be reasonable to assume that the water is supersaturated with respect to N_2. Thus the measured rate of denitrification can be assumed to be a minimum approximation of the rate actually taking place within the BOD bottles. The above errors may counter balance the positive error in measured rate because of the long term effects of bacterial growth in containers (Zobell and

Anderson, 1936) which may increase the measured rate over the *in situ* rate.

Work is presently underway to improve our techniques of measurement and determine some of the variables effecting the rates of denitrification. Determination of *in situ* dissolved nitrogen and oxygen will be done by gas chromatography (Swinnerton, *et al.*, 1962) and a new sampler, which is described in another portion of this report, has been constructed which will obtain close interval water samples for dissolved gas and nutrient determinations.

New 1.0 l reaction vessels have been constructed based on the design of Cline and Richards (1969). Figure 3 shows one of the vessels. The gas sparger allows stripping of O_2 and N_2 from the sample water and the large teflon plug provides displacement of the sample water removed by syringe through the septum. Use of the vessels will allow us to run continuous multiple experiments at the same time. These will include the effects of NO_3 concentration, time, and dissolved oxygen on the rate of denitrification. Subsamples can also be taken for analysis of changes in dissolved gas and nutrient concentration.

Experiments are being conducted to investigate the effects of varying nitrate concentration on the rate of denitrification and to take a closer look at what happens during shorter incubation times. During previous experiments we have added labeled nitrate in excess to that normally found in aquatic systems. This may stress the system and have some effect on the measured rates. We plan to conduct experiments using added nitrate in amounts that approach those found in nature to see if we can detect any dependence of the rate of denitrification on nitrate concentration. Also of great interest is to know what is happening during the first three days of incubation. In future experiments we will measure the rate of denitrification at short intervals during the initial two to three day period. This should show us if the population is already adapted to denitrification and what type of perturbations we find in the rates with respect to time. Another question that should be answered is why the rate of denitrification decreased so sharply when there was plenty of nitrate left. Table 1 shows that although nitrate is significantly decreased in the deep water during the winter stagnation it never goes to zero as it does in Smith Lake (Goering and Dugdale, 1966b). What may in fact be happening is that something such as the energy source, organic carbon in this case, may have become limiting. This should be relatively easy to check by adding excess nitrate, waiting until the rate of denitrification nears zero, then adding a suitable carbon source such as acetate and checking for an increase in denitrification.

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Table 1. Average NO_3-N in μg-at/l for Ace Lake during 1968.

Depth (m)	Winter	Spring	Summer	Fall (mixing)
0.0	Ice	1.4	0.6	2.2
1.0	2.2	2.2	0.5	2.3
2.0	-	-	-	2.8
3.0	1.9	2.1	1.5	2.8
5.0-7.0	1.9	2.0	1.7	7.0

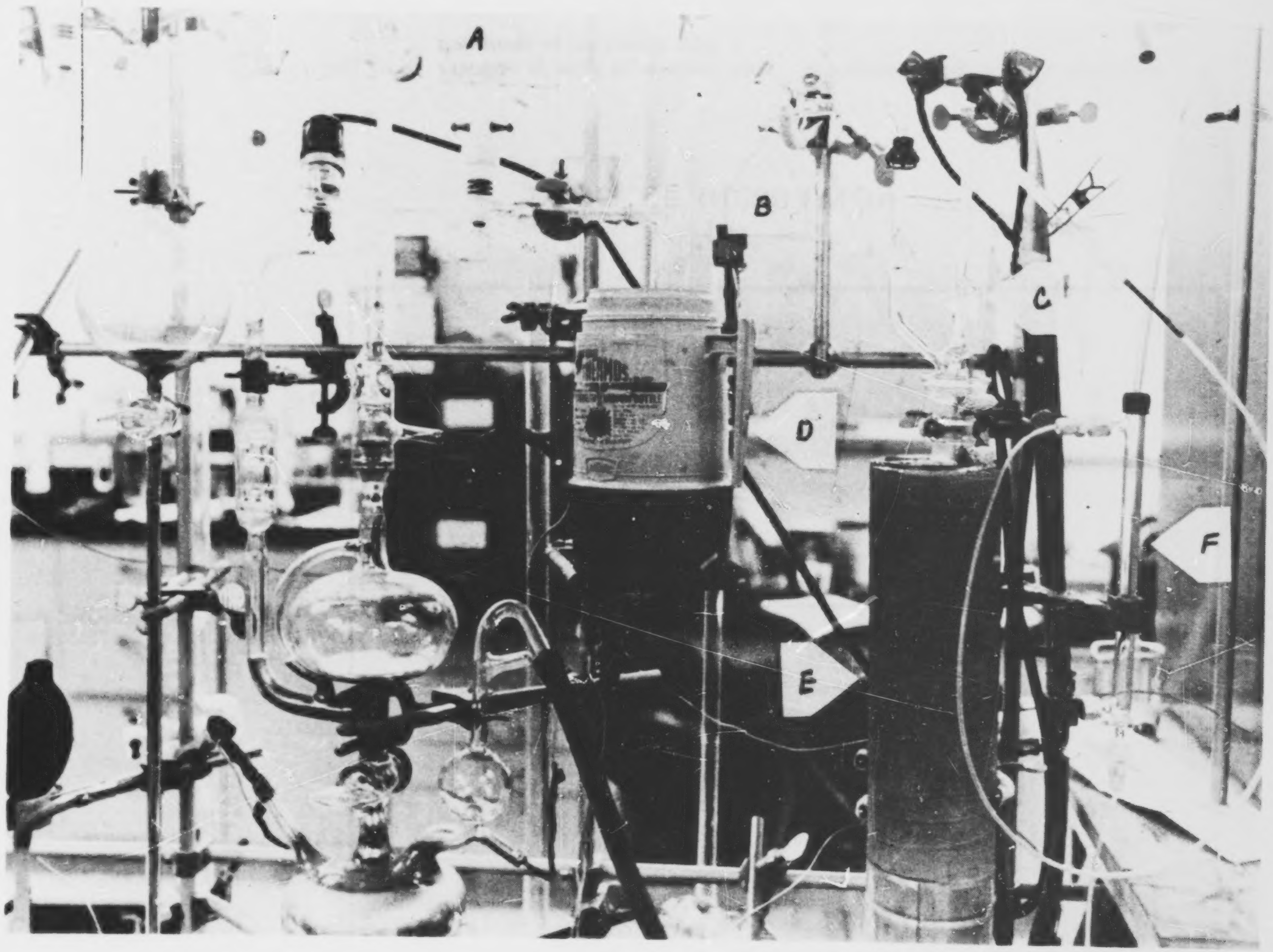

Fig. 1. Gas manifold system for denitrification samples.

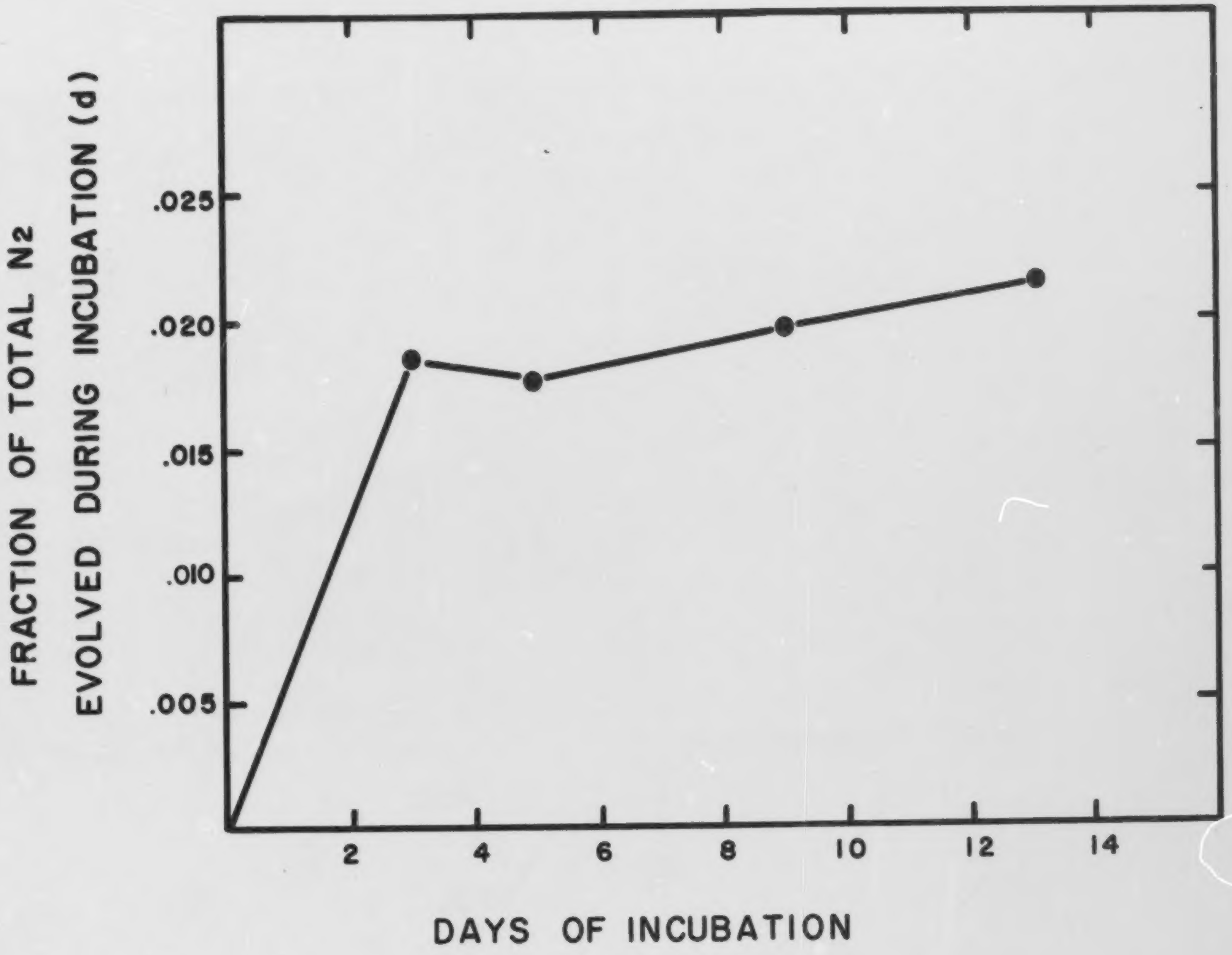

Fig. 2. Fraction of total N_2 evolved from ^{15}N-labeled nitrate in Ace Lake during the winter in the anoxic layer.

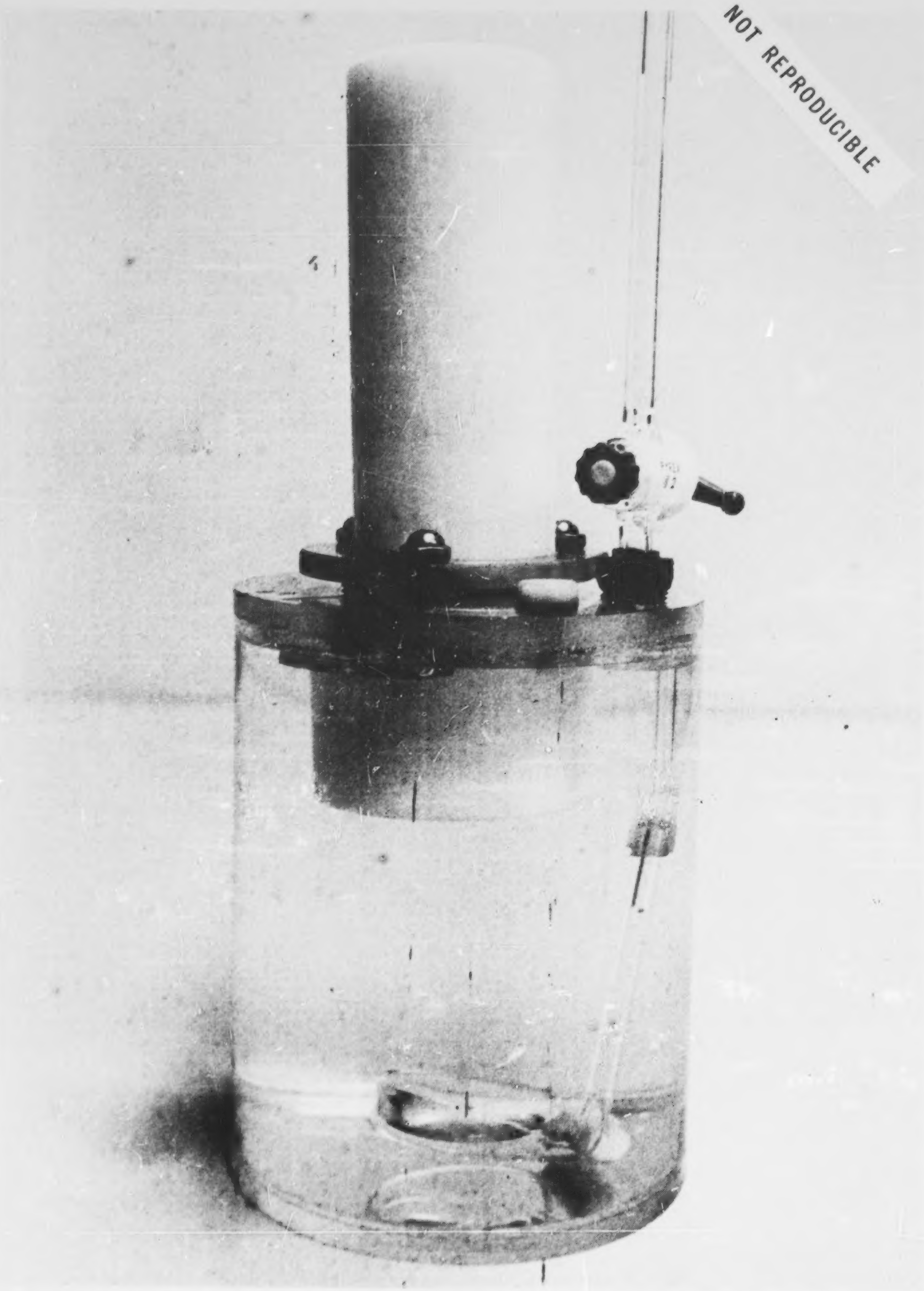

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Fig. 3. Reaction vessels for denitrification studies.

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A CLOSE INTERVAL SYRINGE TYPE SAMPLER

By

R. C. Clasby, W. S. Reeburgh, and Vera Alexander

Studies involving the changes in dissolved gases and inorganic nutrients in an ice-covered lake necessitated the design of a new sampler. After reviewing the numerous commercial and privately designed samplers that have appeared in the literature it was decided that a modification of the type of sampler designed by Broenkow (1969) could be easily adapted. The use of a syringe type sampler gave the small sample volumes that are allowed when dissolved gases are measured by gas chromatography and nutrients by automated techniques.

Because of the requirement to work through small access holes in the ice it was decided to place the syringes in a vertical rather then horizontal position thus giving a narrow profile. As spring actuated mechanisms are not very dependable under freezing conditions a more positive actuating mechanism was designed. This was done by connecting the syringe piston to a rod that could be actuated from the surface. This design was also beneficial in that it allows the operator to flush the syringe by moving the actuating rod up and down, eliminating the necessity to fill the syringe dead space with water of known composition. Operation from the surface also allows precise depth positioning.

The main body of the sampler is thick walled aluminum tubing perforated with slits on alternate sides (Figure 1). An aluminum rod runs through the tubing and is taped for mounting of the actuating blocks. The tubing and rod sections are threaded at appropriate ends for assembly of the three sections. The rod is bent at the top to form a D handle used to pump the syringes and is provided with a thumb-screw lock. The actuating blocks provide connection between the rod and the syringe piston and slide along the slits in the tubing. The cradle is notched to prevent vertical motion of the syringe barrel which is held in place by surgical tubing. Aircraft type hose clamps secure the cradle to the tube and allow alignment of the syringe cylinder and piston.

The sampler is made in three sections that can be assembled in the field. The syringes may be spaced as close as 15.2 cm apart for an effective sampling depth of 2.96 m. The entire sampler, syringes, tools, and spare parts fit in a field case that can be kept warm by hand-warmers to prevent freezing of the samples.

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ACKNOWLEDGEMENTS

The authors wish to express their thanks to Len Weimar, Douglas Marine Station, for his help in design and construction of the sampler.

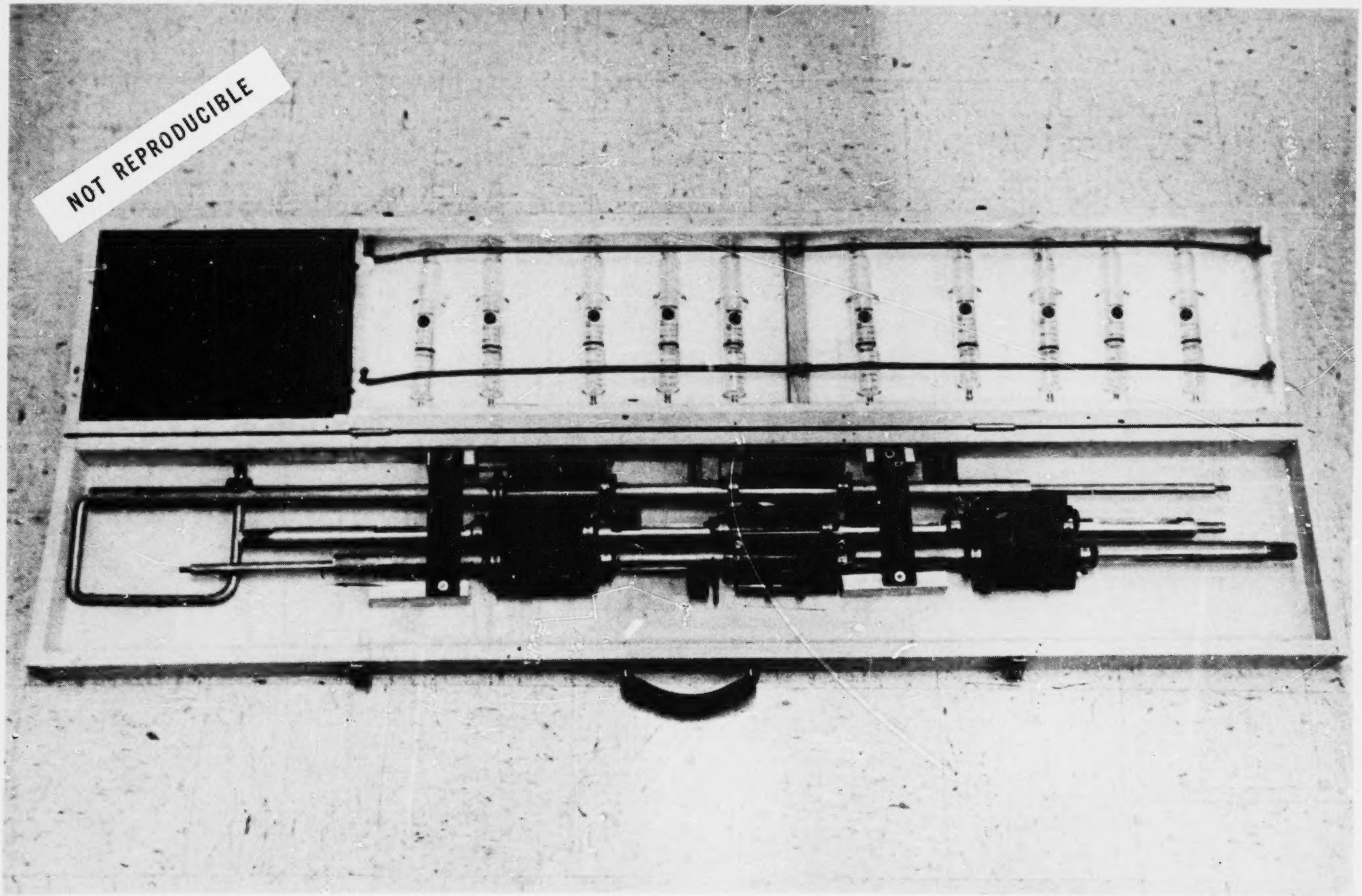
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Fig. 2. Syringe sampler and field case.

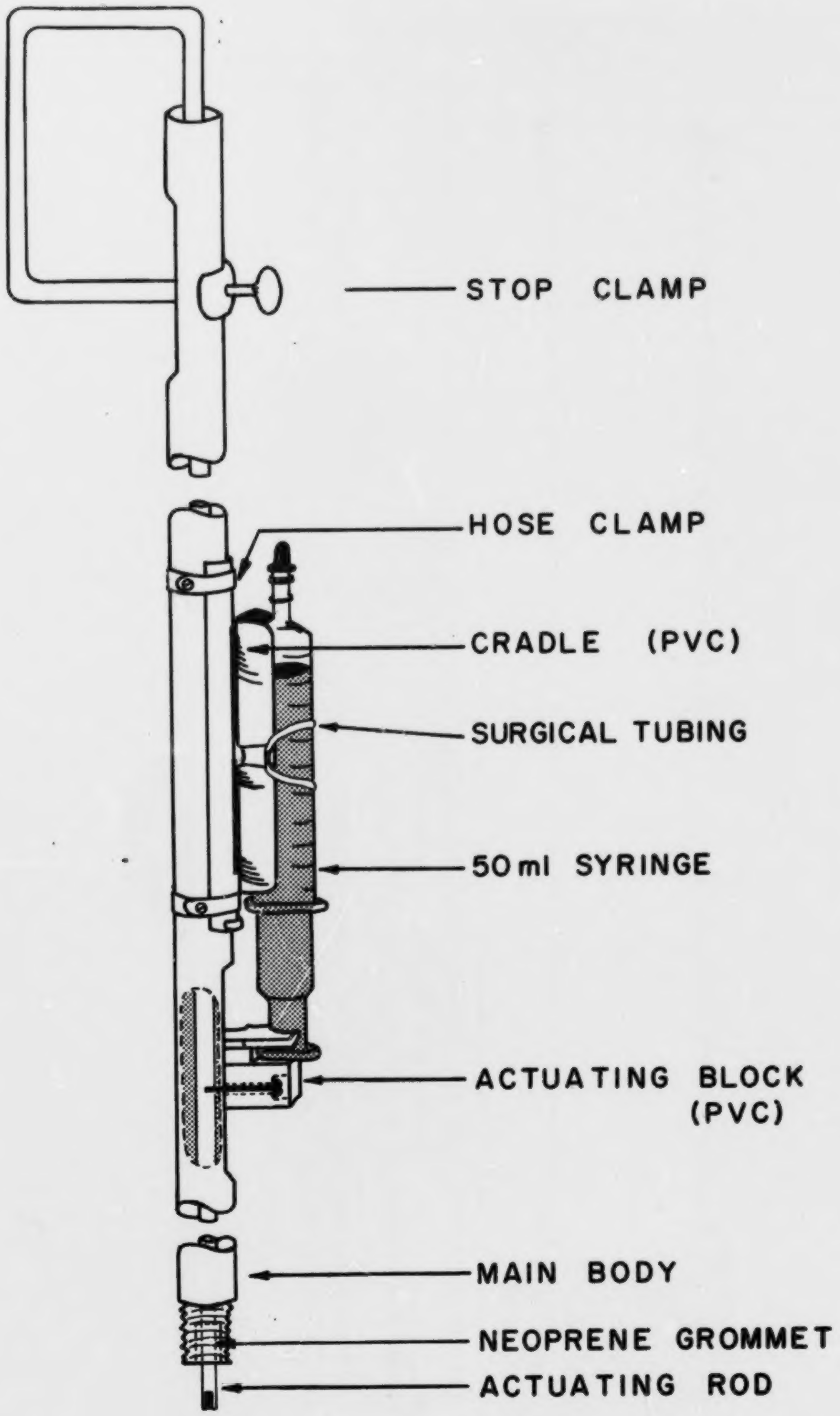
STOP CLAMP
HOSE CLAMP
CRADLE (PVC)
SURGICAL TUBING
50ml SYRINGE
ACTUATING BLOCK (PVC)
MAIN BODY
NEOPRENE GROMMET
ACTUATING ROD

Fig. 1. Syringe sampler.

SECTION FOUR

HETEROTROPHY IN ARCTIC AND SUBARCTIC LAKE WATERS

INTRODUCTION

The problem of heterotrophic growth in natural populations of algae has not been solved, although the evidence against a major role for such metabolism is becoming strong. In arctic and subarctic environments, the problem of light availability is acute during a large portion of the year, and it seems possible that mixotrophy at least may have some significance. The work reported here is preliminary, with a major portion of the effort devoted to method development. However, the results of the few experiments which have been carried out suggest that heterotrophy is not a major mode of metabolism for arctic freshwater algae. However, these studies are continuing, and the work done under F.W.Q.A. funding has laid a foundation for additional work.

STUDIES ON ALGAL METABOLISM IN ARCTIC AND SUBARCTIC LAKES

By

V. Alexander

The limnology of lakes on the arctic slope is inadequately known, and at the same time provides some unique problems due to the stringent physical environment. The work described here is an attempt to augment information about these lakes, with special attention to the biological consequences of the arctic environment on the metabolism of the microflora.

The growth and survival of photosynthetic organisms in regions where long periods of darkness prevail remains an incompletely understood question. In spring, algae in the lakes of northern Alaska are found within the ice cover, at the ice-mud interface and in the water below the ice cover. Whether these algae remain metabolically active during the dark winter months is not clear. If they do, then either they must reduce their metabolic rates to almost maintenance levels, or they must be capable of heterotrophy on a rather large scale.

Heterotrophy in connection with lacustrine phytoplankton populations has been postulated by Rodhe (1955), and investigated by Wright and Hobbie (1965; 1966). Ecological significance for heterotrophy is suggested by the observation that all major groups of algae have heterotrophic members (Provasoli, 1958; Parsons and Strickland, 1962). Although in the open sea the substrate concentrations are considered inadequate to allow a major contribution, in lacustrine situations where freeze concentration of organics operates, the situation may be different. The varying environmental requirements for heterotrophic growth by different algae, such as requirements for oxygen or light, complicate the situation at the species level (Wiedeman and Bold, 1965). However, the question of whether assimilation can take place in the complete absence of light is probably not too important ecologically, since usually some low level of light is available, and the light levels required to support photoassimilation of organic compounds may be quite low. Kalff (1967) has obtained evidence supporting heterotrophy as an important process in a Barrow area pond, and suggests a significant role also in the deeper waters of Imikpuk Lake during the low-light period.

During a previous detailed investigaton of a sub-arctic lake, very few viable algae were found in the water during the darkest months. However, as soon as the day-length and incident light intensity increased, a large population of algae developed under the ice. Although these included representatives of groups known to have heterotrophic potential (*Euglena*, *Chlorella*, *Chlamydomonas*, and unidentified μ-flagellates), there seemed no reason to suggest heterotrophy in this particular case, since no growth was evident in the absence of light. The possibility that organic uptake in the presence of light was allowing a higher growth rate than would otherwise have been possible was not dismissed (Dugdale, 1965). In the arctic marine environment, the earliest growth of phytoplankton appears within the ice cover, close to the ice-water interface. We felt that it would be instructive to look into the arctic freshwater situation also.

The information presented here resulted from part of a broader investigation of the modes of survival of arctic phytoplankton, and represents the freshwater phase of this study. In order to determine the mechanism of growth and survival, three questions need to be answered:

1. Are the particular algae found in this environment capable of using organic substrates?

2. Are the photosynthetic rates adequate by themselves to account for the observed growth?

3. Are organic substrates available in sufficiently high concentrations to allow a significant contribution?

This work was aimed to provide information relevant to the first two questions. Although laboratory studies are ideal for establishing heterotrophic ability, and the physiological basis for any heterotrophy, they cannot tell anything about the actual uptake in nature. We chose to apply combined techniques of radioisotope uptake and radioautography to determine simultaneously heterotrophic potential of the natural arctic populations and to pinpoint the organisms responsible. Concurrent measurements of primary productivity using the carbon-14 technique were run to determine the photosynthetic contribution.

THE RESEARCH SITE

The lakes in the vicinity of Barrow have been described previously by several authors (Brewer, 1958; Boyd, 1959; Comita, 1956 and Kalff, 1967). The study lakes for the work described here included Imikpuk Lake, adjacent to the Arctic Research Laboratory, and Loon Lake, which is adjacent and similar to Ikroavik Lake, although somewhat smaller and shallower. Ikroavik Lake could not be used because overflow water on the surface made it impossible to sample, since this water drained down through any hole drilled through the ice, carrying the ice core with it. Nuwuk Lake, described by Mohr, *et al.* (1961) was also studied, as was a small pond adjacent to a camp and somewhat polluted. We called this latter 'Sewage Pond'. During one days' flying, three stations were occupied, two on medium-sized lakes in the Teshekpuk Lake region, and the third on Sinclair Lake in the same region. These lakes were considerably larger and deeper than the lakes in the vicinity of Barrow. Sinclair Lake had a completely open lead, through which part of the sampling was done. Teshekpuk Lake itself was sampled a few weeks later on two occasions. This lake is the largest in northern Alaska.

The research period covered a time of transition, between June 8th and June 13th, 1969. During the first days there was no sign of thawing, but by June 13th the lakes were covered with overflow and break-up was well underway.

METHODS

For field sampling, a SIPRE corer was used to drill a hole through the ice, and to collect a core. This core was then sectioned, and placed in plastic bags in a styrofoam container. Water samples were either removed from the top of the hole, or a pumping arrangement was used to sample various depths. In the laboratory, the cores were thawed, but kept cool, and aliquots of the various sections were examined for algae and also used in the experimental work. pH, alkalinity and nutrient determinations were carried out using standard methods which are in routine use in our laboratory.

Heterotrophic potential was measured by supplying natural populations of microorganisms with ^{14}C or tritium labeled organic compounds. The activity in the incubation vessels ranged from .016 $\mu c/ml$ to 2 $\mu c/ml$. The amount of substrate added amounted to .016 $\mu M/\mu C$ for ^{14}C glycine, .01 $\mu M/\mu C$ for the ^{3}H acetate, and .004 $\mu M/\mu C$ for ^{14}C leucine. 125 ml pyrex bottles or culture tubes of varying capacity were used for the experiments, and incubation was either carried out *in situ*, in a refrigerator or in a constant temperature room at 5°C. Following incubation, several portions from each bottle were filtered through 0.45 μ pore size Millipore filters (HAWP 025). The filters were washed with appropriate concentrations of unlabeled compound similar to the labeled form used in each particular experiment. In each case, when ^{14}C isotopes were used, one filter was kept for autoradiography, and a duplicate was used for counting.

Autoradiography techniques were as follows. The filters were attached to slides, and Kodak AR10 stripping film was applied, and the slides dried in a light-tight box.

Exposure was carried out in dark slide boxes for periods of time ranging from 20 hours to two weeks depending on the isotope used and the incubation time. Development of the film was carried out in Kodak D19b developer for 2 ½ minutes, after which the slides were rinsed and fixed. The slides were then dried once more, the filters cleared with cedar oil applied through a hypodermic syringe with needle, and examined with a microscope. The work of Brock and Brock (1968) served us a useful guideline in determining isotope concentration required and in developing our darkroom techniques.

Primary productivity was measured using 125 ml pyrex bottles (dark and light). 1 ml of a solution containing 5 μc of ^{14}C bicarbonate was added to each bottle. Following incubation, the samples were filtered through HAWP 025 Millipore filters as above, and rinsed with a dilute HC1 solution. These samples were also occasionally prepared for radioautography to see which segments of the population were responsible for the photosynthetic activity.

Two types of controls were used in connection with the organic uptake experiments. Zero time filtrations were made immediately following addition of the tracer, and these filters examined both by counting and by radioautography. In addition, blank filters were placed under the Millipore filters in the filtration assembly, and counted to check on any adsorption of the organic substrates onto the filters directly.

RESULTS

Radioautography

Preliminary experiments using the radioautography technique were carried out on an ice covered subarctic lake, Smith Lake, in May 1968. A range of tritium-labeled amino acids was tested. The only positive result was the appearance of silver grains on a filament of *Anabaena flos-aquae* which had been supplied with phenylalanine in the dark (Plates 1 and 2). No similar results were obtained with any of the other amino acids. Differentiation between uptake by the algae itself and by bacteria attached to the cell surface is difficult. However, the amino acid is clearly being concentrated in connection with the *Anabaena* filament.

The results of the Barrow tracer work, shown in Table I, indicate that in most cases bacteria attached to detritus and dead algal cells were responsible for the uptake of acetate, glycine and leucine. Uptake of organics by diatoms was observed on three occasions. In Sewage Pond, *Navicula*-type diatoms took up leucine, *Nitszchia*-type diatoms took up acetate, and all diatoms present used glycine. Plate 3 shows a *Pinnularia* or *Navicula* cell which has taken up leucine, and also shows blackened detrital masses. Thus, diatoms from within the mud in benthic environments may depend considerably on such organic substrates. Secondly, in Nuwuk Lake, both algae from the water and from the ice cover used acetate. An algal mat recovered from the base of the ice column in Loon Lake assimilated acetate. Plates 4 and 5 show a diatom demonstrating such uptake. An unlabeled diatom from the same sample is shown in Plate 6. This illustrates how readily it is possible to differentiate between the occurrence and non-occurrence of uptake.

The controls showed that very little radioactivity was adsorbed onto the blank sub-filter, but that zero-time counts may be significant. For example, in the case of leucine supplied to Nuwuk Lake water, a slightly higher count was found in the zero-time sample than following incubation. However, in this case both the counts were low, and may have represented little appreciable biological uptake. In the case of high counts, biological time-dependent uptake is probably responsible. Interpretation of the counts was difficult, since only one incubation time and one substrate concentration were used. Clearly, high counts are not necessarily due to algal uptake.

Primary Productivity

Active photosynthesis was taking place in the lake water below the ice in Imikpuk Lake and Nuwuk Lake, although the rates were relatively low (Table II).

Radioautographs of Imikpuk Lake primary productivity experiments showed that the diatoms were the most important photosynthetic organisms, and that the dark counts must all be due to bacteria, since there was no uptake by diatoms in the dark whatsoever. Not many algae were visible in the water, and most were filamentous blue-green forms. Most of the other lakes, especially the larger ones such as Teshekpuk, Sinclair and Sta. 1, had very low photosynthetic rates. Negative results, with dark uptake much greater than light, were obtained in Sewage Pond, the bottom layer of the ice in Nuwuk Lake, and to a lesser extent in the Imikpuk Lake mud-water sample.

In Sewage Pond, light primary productivity was due to both diatoms and blue-green algae, including *Nostoc* sp. Many *Navicula*-type diatoms were unlabeled. No uptake by algae was observed in the radioautograph of the dark incubated sample, indicating that bacteria were responsible for the dark uptake.

Nutrient and Chemical Results (Table III)

Most of the lakes studied had high amounts of ammonia in the water, suggesting that nitrogen supply is not a problem. With the exception of Nuwuk Lake, phosphate was undetectable. The lakes had appreciable nitrate present, with the exception of Sinclair Lake, which appeared to be rather poor in nutrients, with undetectable levels of silicate. Silicate was present in rather high concentrations in the other lakes.

CONCLUSIONS

The results presented above suggest that in lakes such as Nuwuk, the uptake of organics may proceed simultaneously with photosynthesis, allowing relatively higher growth rates than would otherwise be possible. Organic uptake by diatoms and blue-green algae may also be important in benthic environments. Most of the uptake taking place, however, is attributable to bacteria. The quantitative significance of the uptake by algae cannot be estimated without an idea of the kinds and amounts of organic substrates available in the environment.

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The assistance of Dr. Max Brewer and the staff of the Naval Arctic Research Laboratory is also gratefully acknowledged.

Table I. Results of Organic Uptake Experiments

June 9 - June 13, 1969

	Incubation Conditions	cpm	0 time cpm	Comments on Radioautography
Imikpuk Lake (water below ice)				
^{14}C-glycine, 1 μc/10 ml	light, *in situ*, 24 hr	18695	-	Mostly blackened particles attached to detritus. Diatoms show no uptake.
^{14}C-acetate, 1 μc/60 ml	dark, *in situ*, 24 hr	18695		Several organisms show uptake, especially very small particles.
^{14}C-acetate, 1 μc/60 ml	light, *in situ*, 24 hr	17708		
^{3}H-acetate, 50 μc/60 ml	light, 3 hr, 5°C			Extremely tiny particles labeled.
^{3}H-acetate, 50 μc/60 ml	dark, 3 hr, 5°C			Nothing clearly labeled.
(mud + water)				
^{3}H-acetate, 50 μc/60 ml	light, 3 hr, 5°C			Nothing clearly labeled.
^{3}H-acetate, 50 μc/60 ml	dark, 3 hr, 5°C			Nothing clearly labeled.
Nuwuk Lake (water below ice)				
^{3}H-acetate, 50 μc/25 ml	light, 10°C, 4 hr			Too dense autoradiograph.
^{3}H-acetate, 50 μc/25 ml	dark, 10°C, 4 hr			Clearly labeled diatoms.
(ice core melt, bottom section)				
^{14}C-glycine, 1 μc/10 ml	dark, 5°C, 14 hr	225	23	No visible uptake by algae.
^{14}C-leucine, 1 μc/10 ml	dark, 5°C, 14 hr	40	53	No visible uptake by algae.
^{3}H-acetate, 50 μc/25 ml	dark, 5°C, 14 hr			A few labeled diatoms.

Table I (continued)

Sewage Pond (ice-mud interface)	Incubation Conditions	cpm	0 time cpm	Comments on Radioautography
^{14}C-glycine, 1 µc/10 ml	dark, 5°C, 14 hr	5340	-	Highly blackened filaments (green algae), heavily blackened diatoms.
^{14}C-leucine, 1 µc/10 ml	dark, 5°C, 14 hr	12805	-	*Navicula* type diatoms and some filaments highly blackened. Clear diatoms also present.
^{3}H-acetate, 50 µc/25 ml	dark, 5°C, 14 hr			Very dark autoradiograph, *Nitszchia* highly blackened, *Navicula* not labeled. Some dead filaments labeled due to bacteria.
Flt. Sta. 1				
^{14}C-glycine, 1 µc/60 ml	light, 5°C, 18 hr	526		No obvious uptake by algae.
^{14}C-glycine, 1 µc/60 ml	dark, 5°C, 18 hr	461		No obvious uptake by algae.
^{14}C-leucine, 1 µc/60 ml	light, 5°C, 18 hr	88		No obvious uptake by algae.
^{14}C-leucine, 1 µc/60 ml	dark, 5°C, 18 hr	72		Uptake associated with detrital masses. No uptake by diatoms (*Nitszchia* type) 1 long filament very blackened.
Sinclair Lake (ice core melt, bottom section)				
^{14}C-glycine, 1 µc/60 ml	light, 5°C, 18 hr	618		Diatoms present, but no uptake by these.
^{14}C-glycine, 1 µc/60 ml	dark, 5°C, 18 hr	637		Uptake by bacteria attached to detritus. Many unlabeled diatoms. One diatom labeled.
^{14}C-leucine, 1 µc/60 ml	light, 5°C, 18 hr	86		No visible uptake.
^{14}C-acetate, 1 µc/60 ml	light, 5°C, 18 hr	11355		

Table I (continued)

Loon Lake	Incubation Conditions	cpm	0 time cpm	Comments on Radioautography
(ice core melt, top section)				
^{14}C-acetate, 1 μc/60 ml	light, 5°C, 13.5 hr	11762		Uptake by bacteria attached to detrital masses.
^{14}C-acetate, 1 μc/60 ml	dark, 5°C, 13.5 hr	11762		Nothing clear.
^{3}H-acetate, 50 μc/60 ml	dark, 5°C, 7 hr + 7 hr refrig.	-	-	No detectable uptake.
^{3}H-acetate, 50 μc/60 ml	light, 5°C, 7 hr + 7 hr	-	-	No detectable uptake.
(ice core melt, bottom section)				
^{14}C-acetate, 1 μc/60 ml	light, 5°C, 13.5 hr	11878		Uptake by bacteria attached to detritus
^{14}C-acetate, 1 μc/60 ml	dark, 5°C, 13.5 hr	12264		Same as light above.
^{3}H-acetate, 50 μc/60 ml	light, 5°C, 7 hr + 7 hr refrig.	-	-	Only bacteria attached to detritus blackened.
^{3}H-acetate, 50 μc/60 ml	dark, 5°C, 7 hr + 7 hr refrig.	-	-	Very tiny bacteria-sized particles labeled.
(ice algae)				
^{14}C-acetate, 1 μc/10 ml		13619	-	Not done.
(algae mat)				
^{14}C-acetate, 1 μc/10 ml	light, 5°C, 9 hr.	1965	-	Uptake by bacteria and diatoms.

Table II. Primary Productivity Results (^{14}C Determinations)

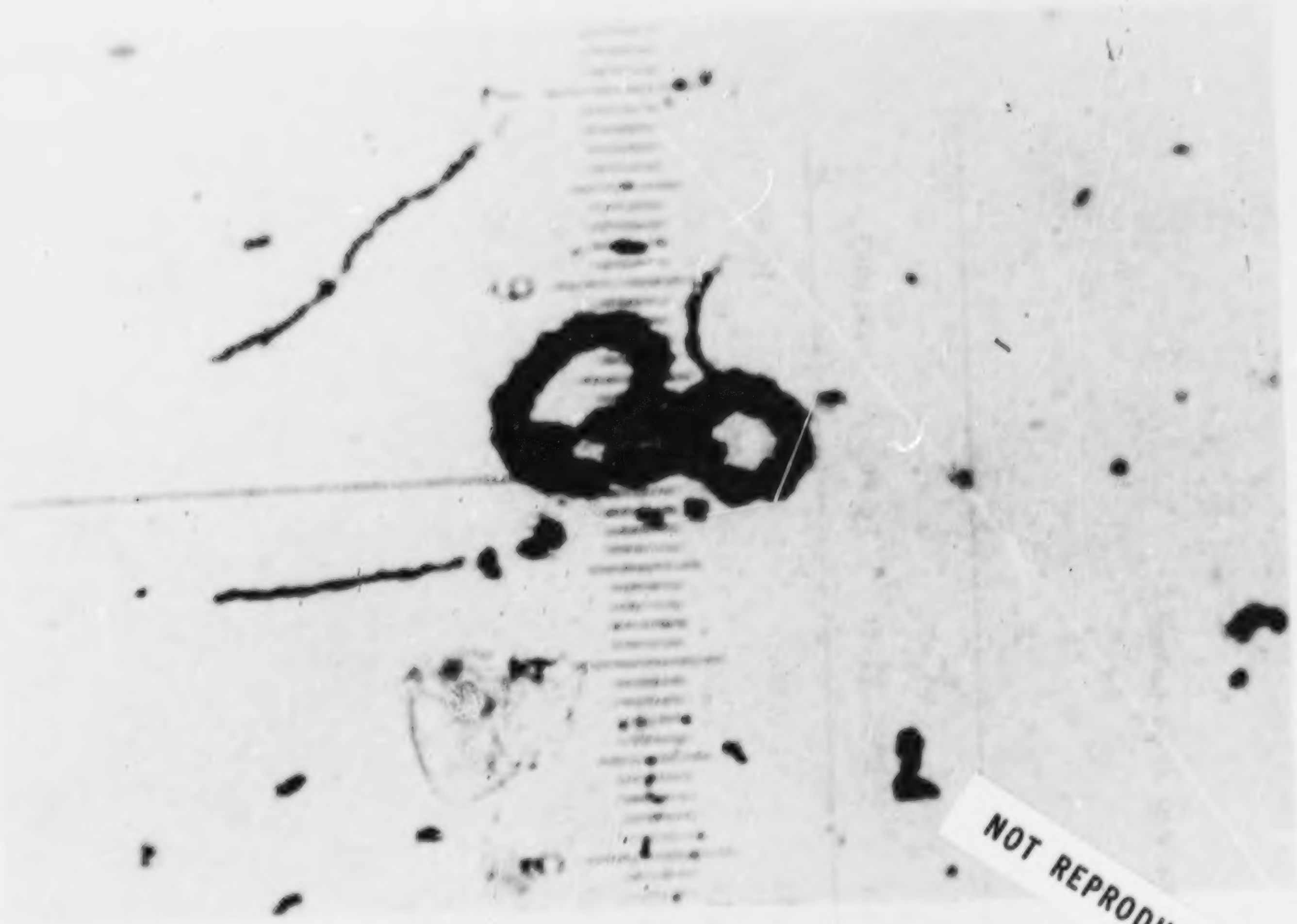
Lake	Incubation Conditions	Light C Uptake µg C liter^{-1}	Dark C Uptake hr^{-1}	Light - Dark
Imikpuk Lake				
(water below ice)	24 hr *in situ*	2.62	0.18	2.44
(water below ice)	3 1/4 hr laboratory	1.33	0.02	1.31
(mud-water interface)	3 1/2 hr laboratory	3.20	4.94	-1.74
Nuwuk Lake				
(water below ice)	4 hr in laboratory	2.56	0.03	2.53
(ice core melt, bottom section)	2 hr in laboratory	3.05	-	$\sim$3.05
Loon Lake				
(ice core melt, top section)	13 hr 5°C, laboratory	0.31	0.09	0.22
(ice core melt, bottom section)	13 hr 5°C, laboratory	0.75	15.55	-14.80
Flt. Sta. 1				
(water below ice)	13 & 19.5 hr laboratory	0.05	0.03	0.02
Sinclair Lake				
(water below ice)	19.5 hr laboratory	0.37	0.38	0.01
Sewage Pond				
	2 hr laboratory	3.87	18.90	-15.03
Teshekpuk Lake				
(water, Sta. 1)	*in situ* 24 hr	0.16	0.06	0.10
(water, Sta. 2)	*in situ* 24 hr	0.15	0.01	0.14
(water, Sta. 3)	*in situ* 24 hr	0.55	0.10	0.45
(water, Sta. 4)	*in situ* 24 hr	0.20	0.12	0.08
(water, Sta. 4)	24 hr laboratory	0.21	0.13	0.08

Table I (continued)

Sinclair Lake	Incubation Conditions	cpm	0 time cpm	Comments on Radioautography
(ice core melt, middle section)				
^{14}C-acetate, 1 µc/60 ml	light, 5°C, 18 hr	14679		
(ice core melt, top section)				
^{14}C-acetate, 1 µc/60 ml	light, 5°C, 18 hr	10035		

Table III. Some Chemical Data on the Barrow Area Lakes

Lake	pH	Alkalinity mg liter^{-1} CaCO$_3$	NO$_3^-$-N	NH$_4^+$-N	NO$_2^-$-N µg-at liter^{-1}	PO$_4^-$-P	Si(OH)$_4$-Si
Imikpuk Lake	6.9	138.5	10.38	4.91	0.00	0.00	10.67
Nuwuk Lake 0 m	6.3	295.6	1.65	10.14	1.14	0.96	7.33
Nuwuk Lake 4 m	6.0	292.5	0.03	7.80	1.09	0.77	14.67
Flt. Sta. 1	6.8	134.10	1.56	8.02	0.33	0.00	4.67
Sinclair Lake	6.0	333.44	0.43	2.56	0.21	0.00	0.00



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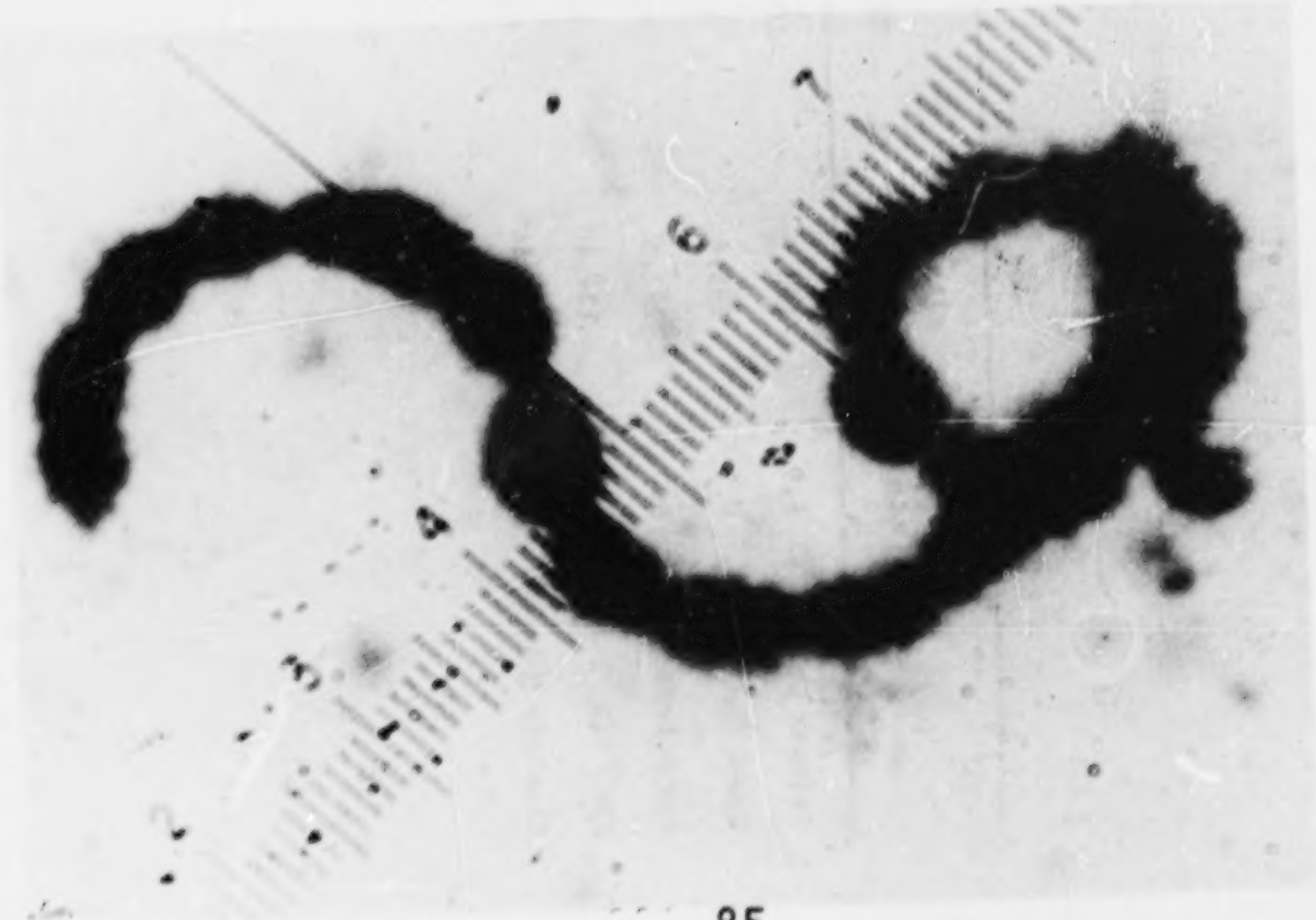
Plates 1 & 2. Radioautograph of Anabaena flos-aquae with tritium-labeled phenylalanine as substrate. From water beneath ice-cover, Smith Lake, May, 1968.



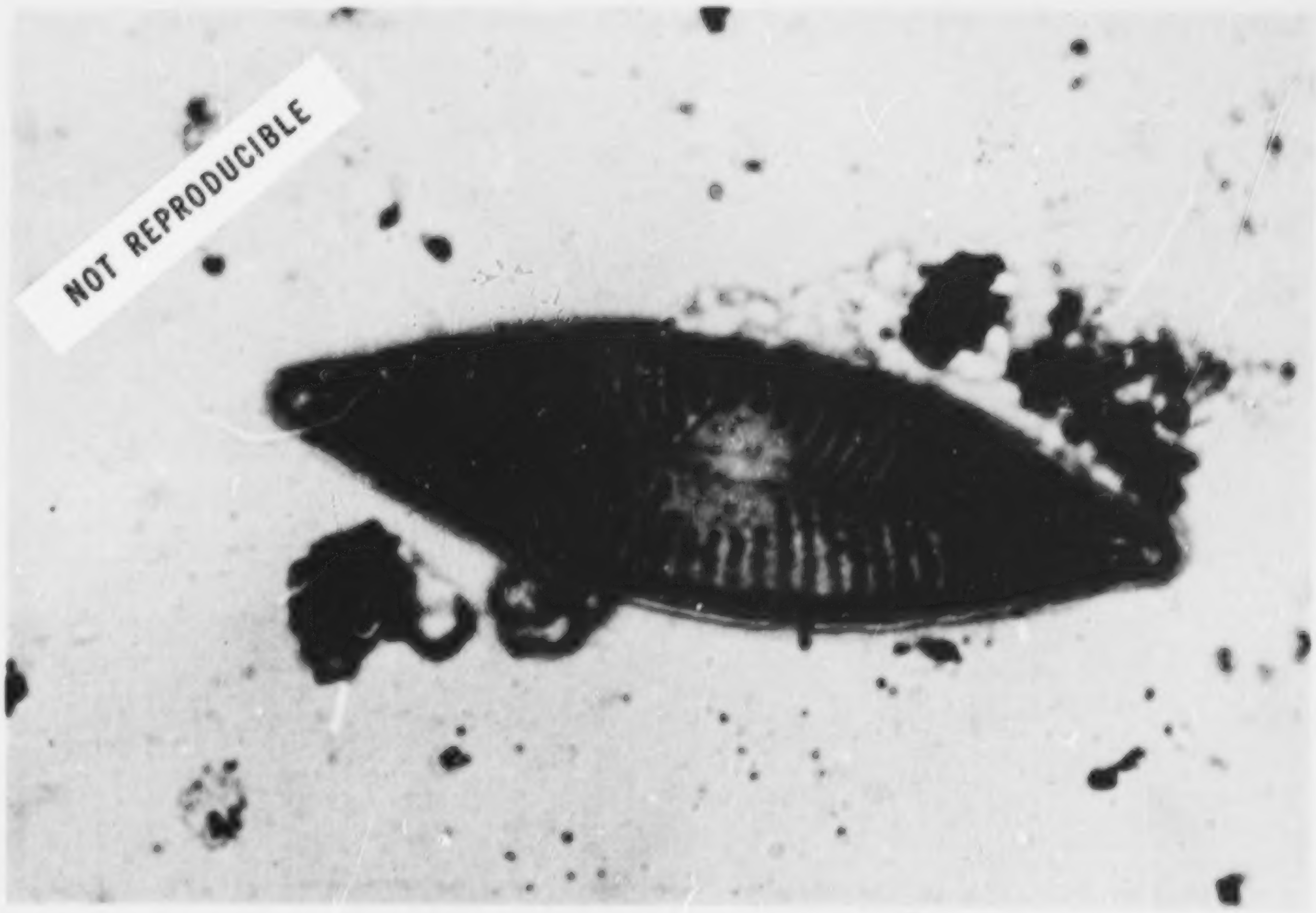


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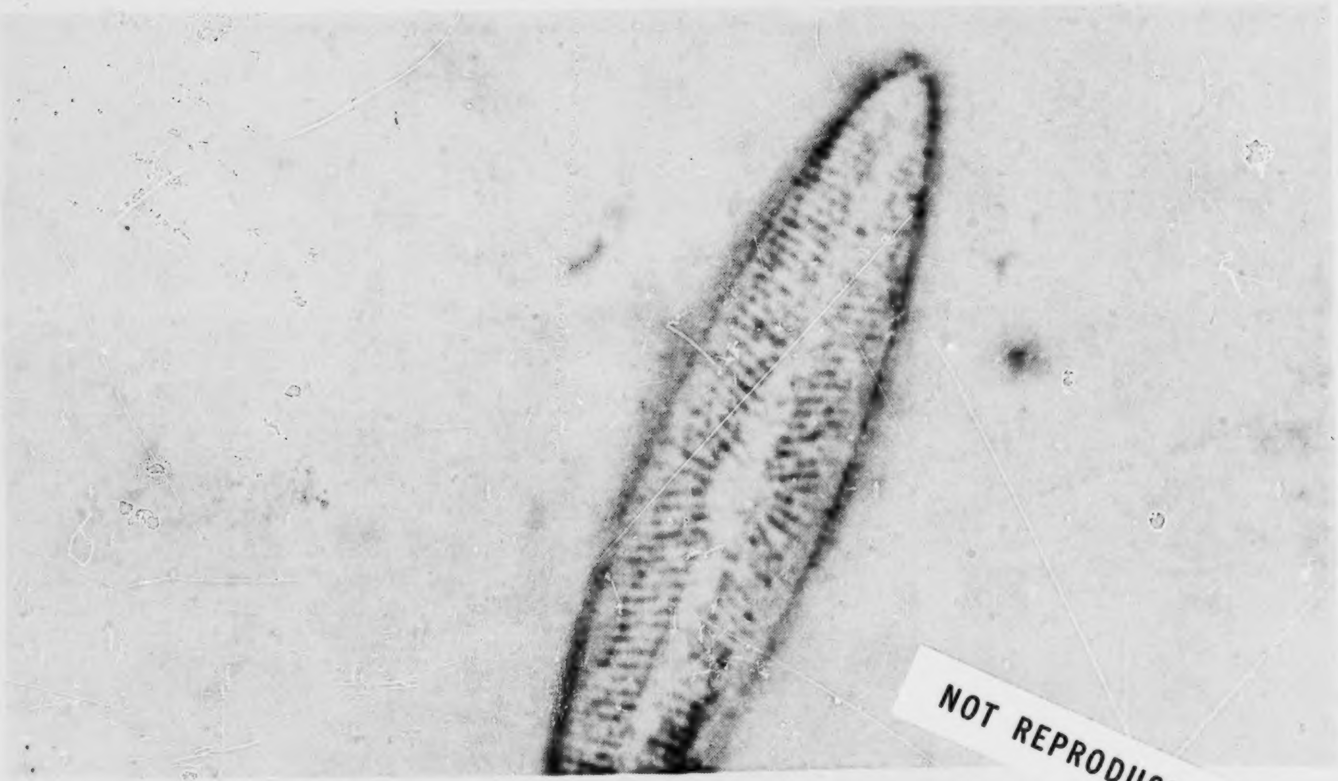
Plate 3. Autoradiograph of diatom which has assimilated leucine.



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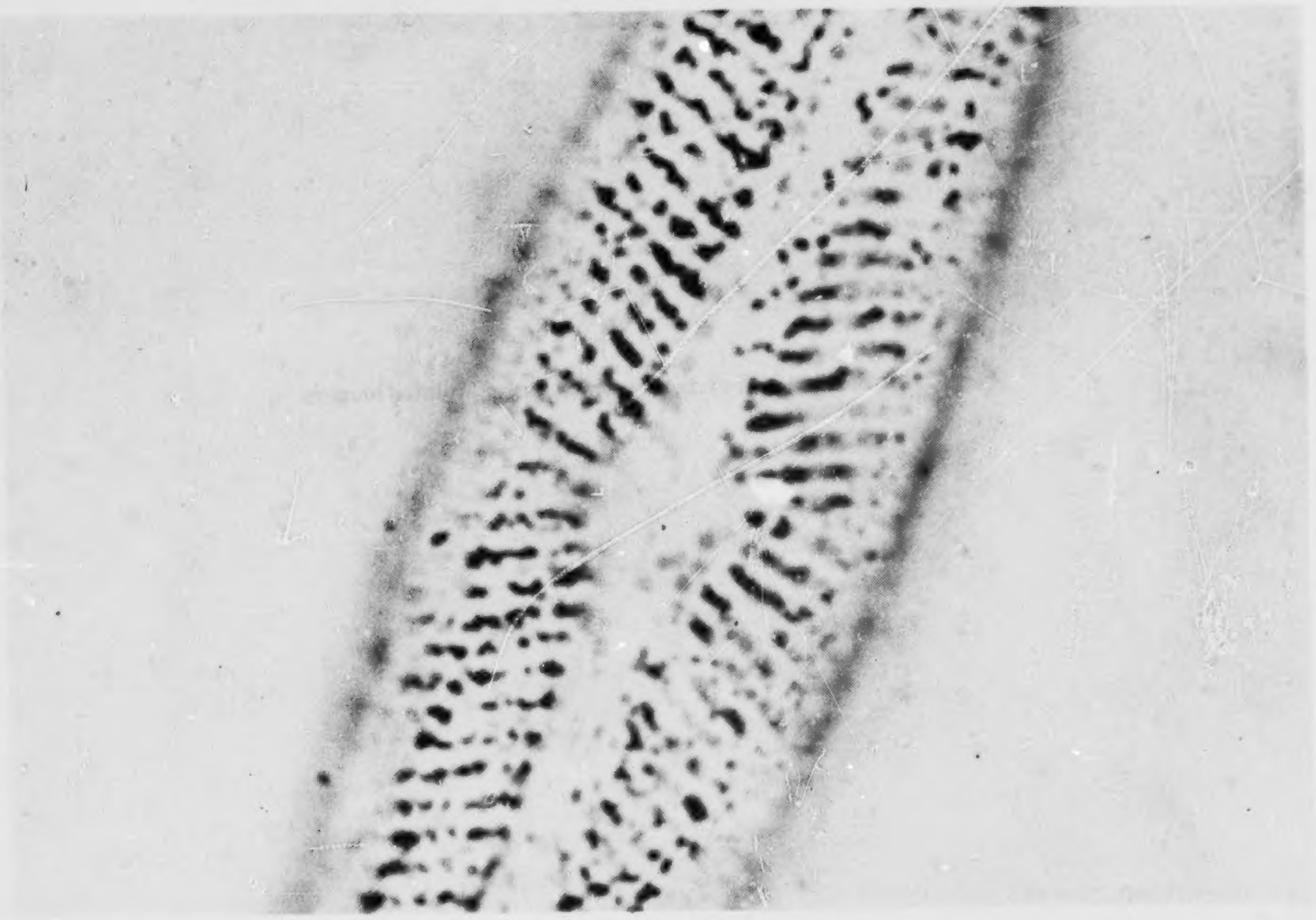
Plates 4 & 5. Acetate assimilation by Loon Lake diatom from the ice-cover.



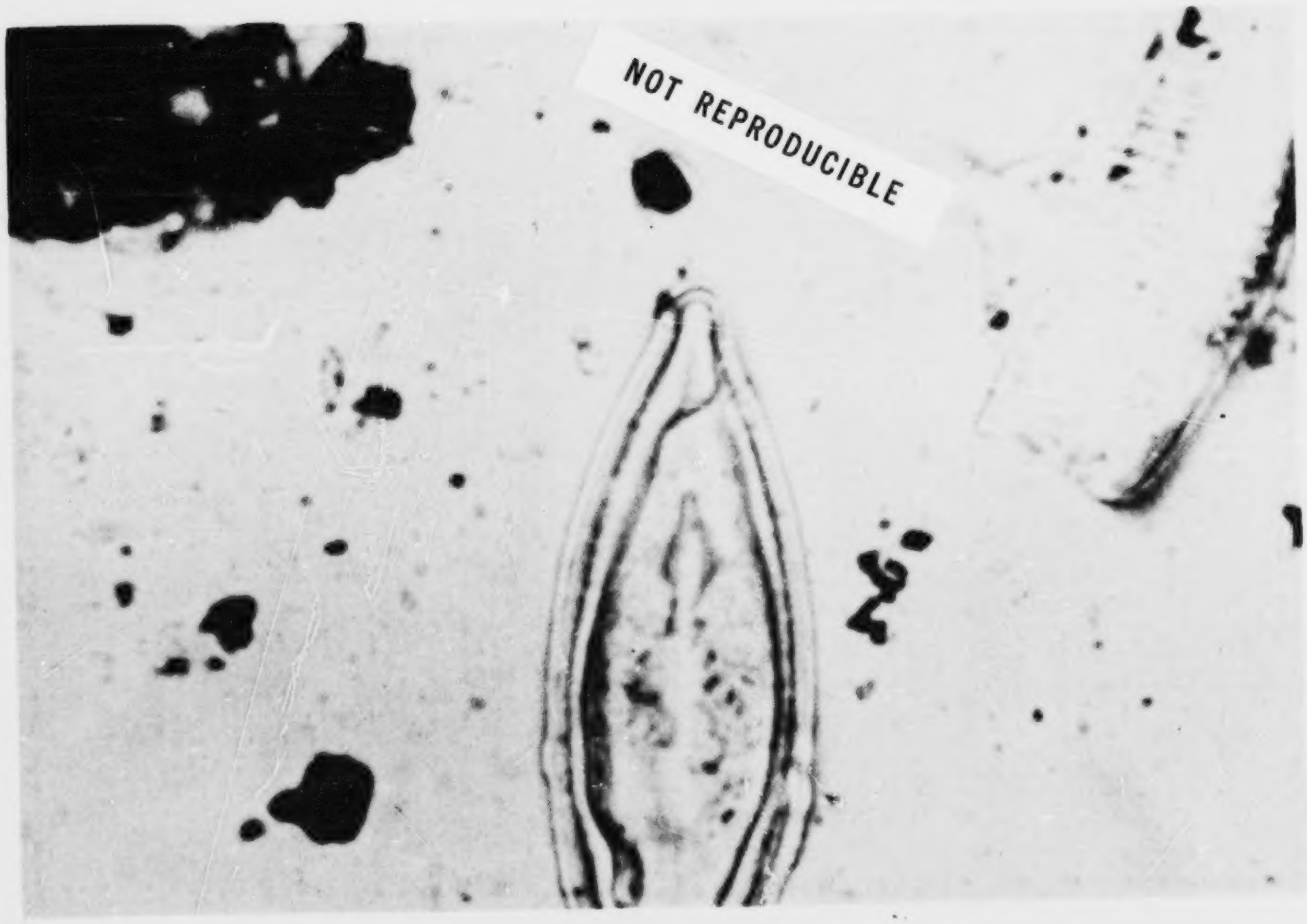


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Plate 6. Unlabeled diatom from Loon Lake ice.

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PHOTOSYNTHETIC ORGANISMS IN SUBARCTIC LAKE ICE

R. J. Barsdate and V. Alexander

While sampling No-name Lake (see Fig. 1), which is located in the Tanana Valley at 63°48′N, 144°35′W, we observed numerous bubbles containing green pigmented material in the bottom 10 cm of the ice cover. Subsequent examination of this material indicated that it is composed of mixed populations of photosynthetic bacteria and algae. This observation differs substantially from previously reported occurrences of organisms in ice.

Recently the ice cover over polar seas has attracted attention as an environment for algal growth. Burkholder and Mandelli (1965) and Fukushima and Meguro (1966) found high concentrations of diatoms in Antarctic sea ice, and photosynthetic production rates as high as 900 mg C/M^3-hours during the austral summer were reported by Burkholder and Mandelli. Well developed diatom populations also exist in the northern polar regions, and chlorophyll *a* levels of above 400 μg/liter have been reported by Meguro *et al.* (1967) in ice sampled near Point Barrow.

The role of ice as an environment for microorganisms has been recognized for many years, although the more spectacular phenomenon of snow brightly colored by algal growths has attracted more scientific attention. The principal organisms in colored snow often have been various species of *Chlamydomonas*, although many other *Chlorophyte* genera, and also *Euglenophyta*, *Chrysophyta*, *Cyanophyta* and *Rhodophyta* have been found in various different colored snows. Some of these snow and ice organisms are facultative snow-dwellers, whereas others belong to the obligate cryoseston. Kol (1968) in her review of cryobiology describes the organisms which have been found in these special environments of snow and freshwater ice.

The under-ice environment of lakes often supports substantial populations of plankton algae, and in several Japanese lakes, Saijo and Sakamoto (1964) reported higher photosynthetic rates below ice cover than in similar conditions with open water. In his work on Peters and Schrader Lakes, which are between 69° and 70°N, Hobbie (1964) found that the annual peak of plankton primary productivity occurred in the spring under clear ice. During April and May, blooms also have been observed under the ice of interior Alaskan lakes, so it appears that organisms are potentially available for the colonization of lake ice.

Assuming the presence of a suitable inoculum in the ice, several factors seems to militate against the development of populations in lake ice. The growing season is shorter than that of the sea ice environment; especially in high latitudes the rate of accretion of ice is rapid, and because of the thermal gradient in the ice the organisms soon would be subjected to rather cold temperatures and no longer would have the interstitial water microenvironment commonly present in sea ice.

No-name Lake is located at the base of a hill and is adjacent to George Lake, one of the larger lakes (7 km long) in interior Alaska. No-name Lake is small, being less than 200 m long and approximately 1.4 m deep at the sampling location. Below the ice, the water (which was only 30 cm deep) was found to contain at most only a trace of dissolved oxygen and was probably anoxic. No sulfide could be detected by smell, a method which has a sensitivity of *ca.* 30 μg H_2S/liter. The water had a specific conductance of 190 micromho/cm at 20°C, a water color of 170 mg Pt/liter and 6 mg dissolved sulfate/liter. No-name Lake was the source of a series of overflows along the margin of George Lake. A number of other overflows nearby on George Lake apparently originated in a wooded area a few hundred meters west of the smaller lake. The numerous overflows suggest the presence of a subsurface aquifer, perhaps driven by hydrostatic pressure from the low hill to the north. If a subsurface source of water is active in the winter in No-name Lake, the pressure drop which occurs when the ground water enters the lake could result in the exsolution of dissolved gases and explain the unusual abundance of bubbles in the lake ice. Other sources of a discrete gas phase, such as methane production in the sediments or the activity of beavers, are possible, however.

In most of the lakes in the region, overflow ice rarely exceeds the underlying clear ice in thickness, and usually the ratio of the thickness of overflow ice to clear ice is *ca.* 1:2. Because of the heat flux through the ice from the lake below, the total thickness of ice should remain relatively constant, depending upon local meteorological factors, while the ratio of overflow ice to clear ice could vary greatly.

On April 8, 1969, the ice cover on No-name Lake was 105 cm thick and consisted of about 85 cm of translucent ice, formed from the freezing of repeated overflows at the upper surface of the lake ice, and 25 cm of clear lake ice formed by freezing downward into the lake water from the ice cover. In this lake the unusual thickness of overflow ice results in a much lower mean accretion rate for the clear ice below than would be expected in this climate. The clear ice contained a number of vertically oriented bubble tubes less than 1 mm in diamteter and up to 2 cm long. These apparently were formed as gas bubbles lying against the underside of the ice were partially excluded during the growth of the ice phase. Also found in the bottom 10 cm of the clear ice were many small subspherical bubbles ranging up to 10 mm in diameter. Those larger than *ca.* 2 mm contained a visible liquid phase below and to the sides of the gas bubble. Since the liquid phase was observed in bubbles which contained no visible organisms, it is likely that the free water resulted from physical processes, probably the local dissipation of radiant energy at the bubble boundaries. The pigmented material was associated with bubbles 0.5 to 10 mm in diameter, and the material appeared both as aggregations in the water film surrounding the bubbles and as a film on the interface between the gas and water phases (see Figure 2).

Microscopic examination of the bubbles revealed a wide variety of organisms but few algae. Most of the material consisted of purple, pink and green colonies of bacteria. A number of minute green filaments were found; these also probably were bacteria. Among the few algae present, one type appeared to consist of various life-cycle stages of *Chlamydomonas*. Some of the small green cells present may have been blue-green algae, but the population was dominated by photosynthetic bacteria.

Photosynthetic bacteria frequently are found at intermediate depths in lakes, adjacent to the boundary between oxygenated and anoxic water. Under these conditions they grow at reduced light levels, often below 1% of the light found in the surface regions (see, for example, Newcombe and Slater, 1950). They thus would seem to be well adapted for growth under the light conditions in the winter ice cover. Photosynthetic bacteria have been observed previously in ice and snow (Kol, 1968). We believe, however, that they have not been described under the particular circumstances encountered here. In this case the organisms were found to be members of complex populations occupying bubbles beneath a meter of ice.

This is the first instance in several winters of work on the lakes of interior Alaska that algae or other pigmented organisms have been observed in abundance in clear lake ice. At times red tinges have been observed in the snow cover of lake ice, and occasionally late in the spring bloom populations have been seen in overflows on lakes, but major growths or concentrations inside the ice near the ice-water interface have not been found. It seems doubtful that the situation found in sea ice is a frequent phenomenon in lake ice at similar latitudes. The combination of factors observed at No-name Lake - the slow rate of ice accretion; the closely related relatively high temperatures and free water in the ice close to the lake water; the abundance of bubbles; and the absence of dissolved oxygen in the lake water - may be responsible for this unusual occurrence of organisms in the lake ice.

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FIGURE CAPTIONS

Fig. 1 Oblique aerial view north from Lake George. Dark areas in foreground are frozen overflows originating from No-name Lake.

Fig. 2 Bubbles in ice from the small lake of Fig. 1 (6x magnification). Several clumps and strands of green pigmented organisms are in the water layer between the large bubble (upper left) and the surrounding ice. In two small bubbles to the immediate right of the large bubble the pigmented material appears as a thin, irregular film on the gas-water interface.

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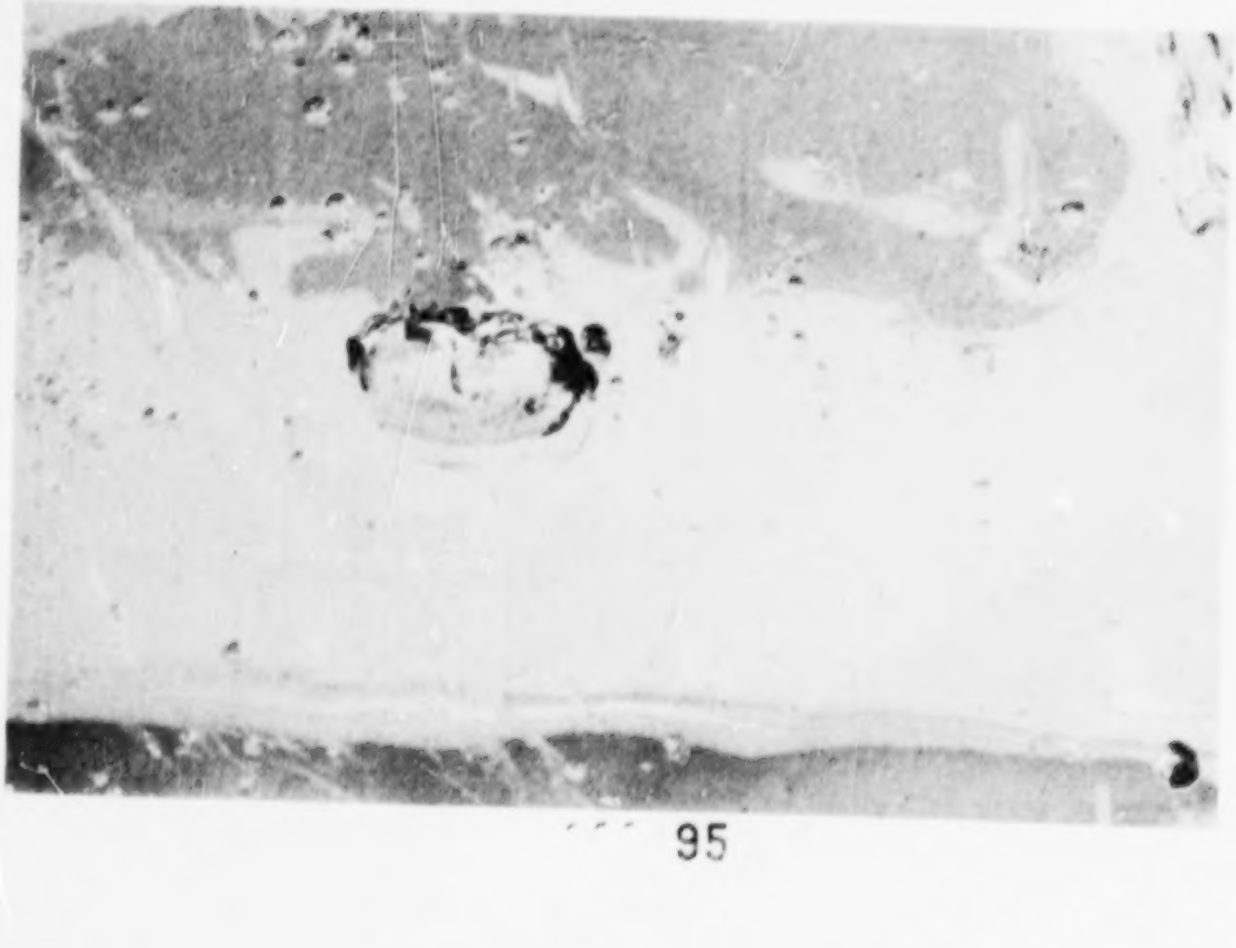

SECTION FIVE

GENERAL LIMNOLOGICAL INFORMATION OF SUBARCTIC LAKES

PHYSICAL LIMNOLOGY, CHEMISTRY AND PLANT PRODUCTIVITY OF A TAIGA LAKE[1]

By

Vera Alexander and Robert J. Barsdate

Institute of Marine Science
University of Alaska
College, Alaska 99701

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[1] Contribution No. XX from the Institute of Marine Science, University of Alaska.

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I. INTRODUCTION

Several arctic lakes have been studied in some detail (e.g. Comita and Edmondson, 1953; Brewer, 1958; Hobbie, 1960, 1961, 1962, 1964; Kalff, 1965, 1967a, 1967b, 1968), and subarctic coastal lakes have also received attention due, in part, to their vital relationship with fisheries (Nelson and Edmondson, 1955; Goldman, 1960; Dugdale and Dugdale, 1961; and Burgner, 1966). Of the arctic lake investigations, only Hobbie's work, and to an extent, Kalff's are comprehensive, intensive seasonal studies, while the other work has tended to emphasize the summer months, or to concentrate on restricted topics. Lakes of the interior region have been much less intensively studied than the arctic lakes and the limitations mentioned above also apply here. In central Alaska the light regime approaches that of the Arctic, with long summer months of insolation, and extended periods of darkness. The winters are colder and summers warmer than either in arctic or in subarctic coastal regions. Although the interior shares many of the rigorous climatic features of the arctic regions to the north and west, it does present a unique environment.

This paper is based on the results of a comprehensive limnological study of an interior Alaska lake. We have attempted to investigate a broad spectrum of properties in as great detail as possible on a year-round basis, in order to provide some preliminary coverage of the limnology of a subarctic Alaskan lake. The data presented here were obtained during several years beginning in the summer of 1963, and although much of the biological work was done during the first two years, sampling and experimental work continued through 1969, with the intensity of effort varying depending on the nature of the information sought. The work has revealed a distinct annual cycle in physical, chemical, and biological regime which appears to be highly reproducible in at least its biological aspects.

II. THE LAKE AND ITS ENVIRONMENT

Smith Lake is located near Fairbanks at a latitude of 65°N, with extreme temperature variations typical of a continental climate. While there are many small lakes and bogs in the area, the climate is dry, with a mean annual precipitation of 30 cm.

During the Pleistocene, glaciers advanced north from the Alaska Range to within 80 km of the area, and wind-transported silt from the nearby Tanana River flood plain formed thick deposits of loess on the surrounding hills. Much of this loess subsequently was retransported into the valleys between the hills. In the valley bottoms the ground now is perennially frozen, often to depths exceeding 50 m, and in the retransported valley-bottom silts the ice occurs in the form of foliated ice wedges and as large subhorizontal masses which probably are buried aufeis. The irregular bottom contours of the deeper portions of Smith Lake, together with its location in retransported silts and its proximity to a number of thermokarst pits, strongly suggest that the lake is cryogenic in origin, having been formed by the melting of one or more massive ice bodies.

The lake is small, having a surface area of 7.2×10^4 m^2, a volume of *ca*. 8×10^4 m^3, and a mean depth of 1.1 m. While there is no permanent inlet stream system, a number of small flows enter the east end of the lake during the spring runoff in May and June and following heavy rains later in the year. These flows have not resulted in regular stream channels, and, even with the most prominent flow (which is indicated as the inlet on Fig. 1), the course across the forest floor is barely discernible by mid-July. The outlet also is ephemeral, although it continues to flow somewhat after the inlet area has dried up. Through evaporation the lake continues to lose water during the summer, and by fall the lake level drops more than 30 cm from its spring high.

The lake occupies a depression in a region of spruce, white birch, aspen and alder forest, which is dry during the summer, but becomes marshy during the spring thaw. The lake is comparatively undisturbed, as it is located in a wildlife study area of the University of Alaska. However, a small portion of the watershed is under cultivation by the University's experimental farm, with three fields located within the watershed. A cultivated field appears as a cleared area with curved tracks running across it in the upper left hand corner of the Smith Lake aerial photograph (Fig. 2). Tilling of this land may result in some disturbance possibly affecting the lake.

III. METHODS

A. Physical and chemical

Samples were taken from a permanently established station over a "deep" basin towards the west end of the lake. This station was marked by a buoy, which also served for suspending samples for *in situ* incubations.

Temperature and light were measured with a Whitney combination probe at depth intervals of 1 m or less. Extinction coefficients (k, as defined by Strickland, 1958) for light were determined graphically from semilogarithmic plots of intensity vs. depth.

Water samples were collected with an opaque, nonmetallic water sampler and protected from direct sunlight during transport to the laboratory. Measurements of pH, alkalinity, and filtration of the samples for water color, chlorophyll, particulate matter, major cations, nutrients and trace metals were performed within 2 hours of sample acquisition. Samples for major cations (calcium, magnesium, potassium, and sodium), for trace metals (cobalt, copper, iron, manganese, and zinc), anionic nutrients (nitrate, nitrite, silicate, and soluble phosphorus) and for chlorophyll determinations were filtered through glass fiber filters (Reeve Angel 984-H Ultra).

Total alkalinity, pH and chloride (specific ion electrode) were determined with a Coleman 37A pH meter, and conductivity with a General Radio Company 1650-A impedence bridge on samples thermostated to 25°C. Dissolved oxygen, total dissolved solids, sulfate and particulate matter were determined following techniques of the American Public Health Association, Inc. (1960), using the azide modification of the Winkler oxygen method, drying 100 ml filtered water samples at 105°C for dissolved solids, and filtration through prewashed, tared 0.45 μ membrane filters for particulate matter.

Measurements for water color were made at 380 nm with a Beckman DU spectrophotometer and converted to cobalt-platinum units (mg Ptl^{-1}) by multiplying the absorbance by a factor of 3000/cell length in cm. This value was obtained from Zimmerman's (1962) data on water color. The numerical values obtained in this manner are not directly equivalent to those obtained by comparison with cobalt-platinum standards and may overestimate the conventional water color determination (American Public Health Association, Inc., 1960) by 20 to 40 percent.

Major cation analyses were made with a Perkin-Elmer 303 atomic absorption spectrometer. Strontium was added to avoid anion interference in the determinations of calcium and magnesium (Angino and Billings, 1967) and sodium was added to samples and standards for the potassium determinations to buffer the ionization interference.

Samples for the analysis of cobalt, copper, zinc, manganese and zinc were concentrated by boiling, wet ashed with perchloric acid, and diluted to 1.00 percent of their original volume. The determinations were made by atomic absorption spectrometry employing corrections for yield blanks and interferences.

Molybdenum was done by a thiocyanate technique following concentration by anion exchange (Barsdate, 1964).

Ammonia was collected in 0.01N HC1 using vacuum distillation or diffusion, and determined by the sodium phenate method of Riley (1953). For some of the later samples, the oxidation method of Richards and Kletsch (1964) was used, and in 1966 isotope dilution (^{15}N) was the routine method. Nitrate and nitrite were done according to Strickland and Parsons (1960), with minor modifications. For nitrate, internal standards were used, and the copper catalyst concentration in the reducing agent was increased tenfold to counteract interference by the high organic content of the water. Reactive phosphorus was measured according to Stephens (1963). Total dissolved phosphorus and total phosphorus were determined by perchloric acid digestion of filtered and unfiltered water samples, followed by sodium carbonate neutralizations and phosphorus determinations as above. Dissolved unreactive phosphorus (DOP) was calculated as the difference between total dissolved phosphorus and reactive phosphorus (DIP), and particulate phosphorus (PP) as the difference between total phosphorus and total dissolved phosphorus. Reactive silica was determined as a silicomolybdic acid (Grasshof, 1964) on a Technicon autoanalyzer.

Particulate nitrogen was measured using a Coleman nitrogen analyzer. Glass fiber filters were used to collect the particulate material from a volume of lake water; the filter was dried and ground with a mortar and pestle prior to introduction into the combustion tube of the analyzer. For the determination of chlorophyll *a*, glass fiber filters and their associated particulates were macerated in 90% acetone and extracted in the dark at 3°C for 24 hours. After centrifugation the absorbance of the extracts was measured at 658 nm and chlorophyll *a* estimated according to Dugdale (1965).

Sediment cores were obtained in 4.5 cm diameter lucite tubes equipped with small plastic check valves. A lucite tube was taped to a 1/2 inch aluminum rod and lowered through a hole in the ice. The action of the check valves and the friction of the sediment were sufficient to retain samples in the coring tube without the use of a core-catcher or other restricting device at the bottom of the tube. Sections of core material were weighed in tared beakers, dried for 48 hours at 105°C, cooled in a vacuum dessicator, and reweighed.

For the chemical analysis of the sediments, 3 to 4 g of dried sample was refluxed with perchloric acid (3 ml of 70% $HC10_4$ per g material). Prior to digestion *ca.* 6 ml of distilled water was added to each sample to moderate the initial stages of the reaction. After the digestions were complete, the samples were diluted to 25 ml and the particulate fractions separated by centrifugation, washed, dried and weighed. The wash water and digestion solution were combined and diluted to 25 ml per g of original sediment. Co, Cu, Fe, Mn and Zn were determined from these solutions by atomic absorption spectrometry, and P was determined spectrophotometrically as phosphomolybdic acid after neutralization with ammonium hydroxide (Strickland and Parsons, 1965).

Organic carbon was converted to CO_2 by wet oxidation with persulfuric acid (Mackereth, 1963) and the CO_2 determined conductimetrically after reaction with barium hydroxide.

B. Biological

Phytoplankton

Photosynthetic carbon fixation was measured by the ^{14}C method (Steemann Nielsen, 1952). Light and dark bottles were incubated *in situ* for either a 24 hour period, or for 3 or 6 hour periods. On some occasions, additional incubations under different conditions were carried out. Following incubation, the samples were filtered (Millipore HA membrane filters, 0.45 μ pore size), rinsed with 5 ml of dilute (0.005 N) HC1, and dried for subsequent radioactivity assay. Total available carbon was calculated from pH and alkalinity. Phytoplankton samples were examined both in fresh samples and in samples preserved with Lugol's solution (Verduin, 1960).

Epiphytes

The sampling location was approximately at the center of the lake in 3 m of water. The station consisted of nonmetallic float anchored with a plastic line on which were threaded five 500 ml polyethylene bottles spread at 0.5 m intervals from the surface to a depth of 2 m. Vertical slits were cut in the bottles, and glass microscope slides were inserted so as to project radially from the axis of the line.

After the desired incubation period, the slides were removed, drained briefly, and stripped of the accumulated material. For chlorophyll determinations the material was macerated and then extracted with 10 ml of 90% acetone in darkness for 24 hours. After centrifugation the concentration of chlorophyll *a* was determined by the method of Richards with Thompson (1952) employing the equations and correction for turbidity recommended by Parsons and Strickland (1963). The entire process was carried out in duplicate with one side of a microscope slide (13.75 cm^2) constituting a sample. The relative standard deviation was ± 10%, n = 45 pairs, and includes both the analytical uncertainty and sample inhomogeneity.

Macrophytes

From six approximately equidistant points around the lake perimeter, transects were established extending into the deeper portion of the lake. Benthic plant samples (0.25 m^2) were obtained at water depths of ~0.25, 0.75, and 1.25 m on each transect. The collected material was sorted, weighed wet, and weighed again after oven drying at 90°C. Oxygen evolution was determined from the change in dissolved oxygen in 300 ml BOD bottles containing 2 to 3 g (wet weight) segments of actively growing plants. To remove phytoplankton and reduce the oxygen concentration to prevent subsequent supersaturation, the water first was filtered (Whatman No. 4) and then was siphoned into the BOD bottles in which the plant material previously had been introduced. Initially the dissolved oxygen concentration was 5.2 mg l^{-1}, less than 60% of the saturation value. The samples were incubated for two hours at 20°C under mixed fluorescent and incandescent light at an intensity of 20,000 lux. Oxygens were determined by the Alsterberg Winkler techniques.

IV. THE PHYSICAL REGIME

A. Annual thermal cycle

The ice-covered period has terminated consistently between 25 May and 29 May during seven years of observation. The thermal pattern in the water following the ice "break-up" varies considerably between different years, since conditions of wind and insolation at the time of melting markedly influence the degree of establishment of thermal stability during the early part of the summer. The days at the end of May and during early June are often sunny, and the long hours of sunlight at this latitude, coupled with low wind velocities, lack of rainfall, and limited penetration of light favor the generation of a stratified temperature profile, and therefore, there is a tendency for the lake to mix only partially in spite of its limited depth. In 1963, however, the lake mixed immediately upon "break-up" (Fig. 3). Such variations have considerable biological and geochemical implications, since when mixing is incomplete, the surface water layer is poorer in nutrients and contains much less organic material than the layer below both as a result of its partial origin as ice and of the reduced advection from below related to the increased stability of the water layer. The total amount of the nutrient substances available to the June algal bloom is thus much lower. Stratification does tend to break down to some extent during the summer, although strong mixing seldom reaches the bottom layer immediately adjacent to the mud surface. Maximum surface temperatures can occur within about two weeks of the ice disappearance, and cooling begins during July and proceedes slowly during the late summer. The surface water reaches 0°C at the end of October, and from this time ice-cover persists until the end of May, with the ice normally attaining a maximum thickness of 0.7 to 0.8 m (Fig. 4). The bottom water remains around 3.8°C during the entire winter.

The seasonal temperature distributions thus follow a rather consistent pattern, with a rapid climb to the first maximum followed by some cooling, which may be due to some extent to mixing of deeper water with the surface layer. There tends to be a second maximum in mid-July, following which there is a steady cooling accompanied by intensified mixing, so that by mid-August the lake is isothermal down to 2 m. These relationships can be seen in Figure 3, where the three years of temperature data shown illustrate many of the points discussed above.

B. Heat budget

As expected for a small shallow lake, the heat budget of Smith Lake is quite low. As indicated in Table 1, the annual heat budget for the water of the lake is only 6,857 g cal cm^{-2} yr^{-1}, of which 75% or 5,177 g cal cm^{-2} is the winter heat. The largest single factor in this budget is the latent heat of melting of the ice, which accounts for over 60% of the annual heat gain of the lake water.

Another common characteristic of the thermal regime of small lakes, a relatively high sediment heat budget, is apparent in Smith Lake. At a water depth of 2 m the annual range of surface sediment temperature is 15°C, and thermal gradients on the order of 6 to 8°C are present in the upper meter of sediment following "break-up". While we do not have sufficient data to calculate a heat budget for the sediments, it is undoubtedly higher - perhaps by as much as 2 or 3 fold - than the summer heat budget for the lake water.

C. Optical properties

Smith Lake water is deeply colored by brown dissolved organic matter, and as a result the penetration of radiant energy is quite limited. The attenuation is particularly strong at the shorter wave lengths, and maximum transmission occurs at 700 nm. The sestonic component of attenuation always is small in comparison with the dissolved component, and during the winter months water color and absorbance determinations of filtered and unfiltered samples are nearly identical.

Water color (which is treated in more detail in the following chemistry section) and light extinction (Table 2) tend to be high in the winter and lower in the ice-free period. A secondary high in light extinction occurs during and following the spring plankton bloom, and a slight increase also occurs toward the end of the autumnal circulation. The variations are limited, however, and the depth of 1% of incident light usually is within the range of 1.7 ± 0.5 m.

The absorbance of water collected from the lake on 11 November 1969 is plotted in Fig. 5, and the absorbance of distilled water and water from Adelaide Lake, a moderately colored (28 Pt units) Northern Wisconsin Lake (James and Birge, 1938), have been included for comparison. Curves of solar flux as a function of depth were constructed for the same waters (Fig. 6), calculated from the spectral composition (Howard *et al.*, 1957), and mean solar radiation for June (U.S. Weather Bureau, 1961-1966) at Fairbanks, Alaska, and the absorbance data of Fig. 5. Absorbance data for distilled water was used for all three waters in the range 800-2140 nm.

The radiant energy flux at 1 m in Smith Lake is very low (less than 10 g cal cm^{-2} day^{-1}), and during the interval between "break-up" and maximum water temperature (*ca.* 50 days) roughly 1.7×10^{11} g cal of radiant energy pass through the 3.4×10^4 m^2 area included in the 1 m depth contour of Smith Lake. If it is assumed that all of this energy is dissipated on the 2.6×10^4 m^3 of water present at depths greater than 1 m, the mean water temperature rise would be <7°C or *ca.* 50% of the observed temperature rise. When the unassessed but presumably large heat flux into the sediments also is considered, it is evident that advective processes are the most important factors in the transfer of heat to the deeper waters of the lake. In the hypothetical case of the basin of Smith Lake containing water with the properties of Adelaide Lake, the calculated temperature rise in the water below 1 m (ignoring advection and losses to the sediments) would be 45°C. From this it seems likely that the intense thermal stratification that exists in Smith Lake is in large part due to the colored organic matter present in the water.

V. CHEMISTRY

A. Major components

The most abundant cations in Smith Lake are calcium, magnesium, and sodium, all of which occur at similar levels (Table 3). The usual cation progression for interior Alaskan lakes is Ca>Mg>Na>K (Likens and Johnson, 1968); in Smith Lake the abundance of calcium is lower, and sodium higher than might be expected. Of the inorganic anion components bicarbonate is dominant (*ca.* 30 mg $CaCO_3$ l^{-1} during the summer), with sulfate and chloride together amounting to 2 or 3 mg l^{-1} at most.

The exclusion of dissolved substances from the ice during freezing produces a seasonal cycle in which the concentrations of conservative components rise as the ice thickness increases, and during the winter alkalinity, dissolved solids and conductivity increase to roughly twice their summer values (Table 4). Year-to-year variations in the spatial distribution and concentration of major components are caused by precipitation levels and the presence or absence of stratification immediately following spring breakup of the ice. The absence of normal circulation in 1964 resulted in a period of intense chemical stratification beginning in early May and extending into July (Fig. 7 and 8).

For most of the year the amount of particulate matter in the lake is quite low (<1 to ~3 mg l^{-1}), a condition which reflects the poor development of the inlet stream system. Suspended particulates increase to *ca.* 4 mg l^{-1} during the circulation which occurs at the end of May, decline briefly, and again increase during the spring bloom to the annual high of 5 to 15 mg l^{-1}. A slight increase also occurs during the period of autumnal circulation.

A number of determinations for dissolved organic carbon were made on Smith Lake (Table 5), and of these the mean carbon concentration was 31 mg l^{-1}. The precision of the analytical procedure precludes a detailed interpretation of these data, but there is some suggestion that the concentration of dissolved organic carbon increases during the winter, as dissolved organic substances like inorganic ions are excluded from the ice during freezing. About 60 mg l^{-1} (ash-free dry weight) of yellow-brown organic material can be extracted from acidified Smith Lake water with *n*-butanol. This material has been freeze-dried, redissolved in a slight excess of potassium hydroxide and back-titrated with a strong acid. The resulting titration curve (Fig. 9) suggests that under the natural lake conditions (pH $\simeq$7; total cations $\simeq$1.1 meg l^{-1}), substantial quantities of the major cations are bound in association with the dissolved organic fraction of the lake water. Ghassemi and Christman (1968) have examined the colored organics from Smith Lake; they appear qualitatively similar to the organic constituents of water from more temperate environments.

B. pH and dissolved gases

Although highly colored and rich in dissolved organic matter, Smith Lake is not a typical bog lake in that it is nearly neutral in pH. During the winter the pH is usually between 6.7 and 6.9 and during the summer values below 7.0 usually are associated with low oxygen water in the hypolimnion. Poorly buffered melt water with pH range from 6.0 to 6.6 occurs in the lake from the beginning of the thaw (around May 1) to the spring bloom in the second week of June. Inorganic carbon assimilation during the spring phytoplankton bloom produces a sharp rise in pH to values approaching 10 which is followed by a sharp drop to summer values of *ca*. 7.5 (See Fig. 10).

The dissolved oxygen levels in Smith Lake are variable, changing in response to wind stress as conditioned by thermal and sometimes chemical stratification. The biochemical oxygen demand in the lake is quite high, as dissolved oxygen is depleted rapidly in the deeper waters during periods of restricted circulation. Even the surface waters of the lake seldom appear in equilibrium with atmospheric oxygen and, with the exception of localized areas in heavy stands of benthic plants, oxygen concentrations are substantially below saturation values except during the brief period from the breakup of the ice through the spring bloom. From mid-June until early October the dissolved oxygen in the upper water remains in the range of 60 to 80% of calculated saturation values.

At depth, oxygen starts to decline with the formation of the winter ice cover, and the lake eventually becomes completely anoxic, usually during the month of February. In April dissolved oxygen has been observed in association with under-ice plankton blooms, but observed duration of both blooms and the oxygen is only a few days. In early May oxygen again appears below the ice in a layer chemically distinct from any other water found in the lake during the remainder of the year. This water is characterized by fairly low conductivity and dissolved solids, a low alkalinity:dissolved solids ratio, and high phosphate, nitrate, and silicate concentrations (Table 6). The low alkalinity suggests formation largely from melted snow. Thus the oxygen found under the ice in the spring probably is the result of both biological productivity and mass transport of oxygenated melt-waters down through fissures in the ice.

After the disappearance of dissolved oxygen from the lake during the winter, sulfide occurs in the deeper waters. By March sulfide is present at all levels but in April retreats down from the ice to a depth of *ca.* 1 m and disappears entirely during the circulation that takes place as the ice cover is completely removed during the last week in May. Anoxic water sporadically occurs during the summer at depths greater than 2 m, and sulfide usually is associated with these occurrences. When present, sulfide was found in concentrations of less than 0.20 mg l^{-1}. The rather low sulfide concentrations which occur with reducing conditions are probably not due to low levels of microbial metabolism but rather to the lack of availability of sulfate and organically bound sulfur. Neither sulfate nor total sulfur appears above the limits of detection (*ca.* 2 mg SO_4 l^{-1} in Smith Lake).

C. Nutrients

The trend towards extreme variation with season held for the dissolved nutrient compounds in Smith Lake water. The lake did not seem in general to be poor in nutrients, although levels did decline during peak of phytoplankton production. All available information dealing with nutrient concentrations is presented in one table, covering the years 1963, 1964 and 1966 (Table 7). Oxygen concentrations are incorporated into this table because they are highly relevant to the seasonal distribution of the nutrient compounds.

Nitrogen

Nitrate was not generally an abundant nitrogen form in Smith Lake, although it did tend to accumulate gradually in the fall and winter. Since there was no appreciable income of water to the lake during this time, this increase can be attributed to a steady rate of nitrification of ammonia released from the organic nitrogen fractions within the lake water. Such production of nitrate is not balanced at this time of year by significant biological removal. Upon the depletion of oxygen in the water, which took place in late February or early March, all the accumulated nitrate disappeared. Denitrification, the dissimilatory reduction of nitrate in the absence of oxygen, has been shown responsible for this decline (Goering and Dugdale, 1966). From this time till May, only traces of nitrate were detected in the water. Immediately upon the reappearance of oxygen, nitrate was found once again in low concentrations. The data in Table 7 show that the actual timing both in the early spring depletion and in the fall increase varied considerably from year to year. Nevertheless, the general pattern held. The 1966 data may be considered the most reliable, since the numerous problems involved in carrying out this determination in the highly colored Smith Lake water had been resolved by this time (see the methods section above). During the summer months, the nitrate levels remained rather low, close to the lowest limits of detection, with only occasional short-lived increases.

Ammonia was the most consistently abundant nitrogen source in Smith Lake water, detectable at most times with the exception of only short periods of time during phytoplankton production peaks. For example, although ammonia was absent from the surface water during the June bloom in 1963, it reappeared rapidly after the bloom had declined. Similarly, the reduction in ammonia content under the ice in May has been shown due to biological uptake by a population of μ-algae (Billaud, 1968). The combined nitrogen reduction will be discussed further below in connection with the primary productivity. The overall yearly pattern shows an increase in fall and winter, with a great acceleration in the rate of increase upon the onset of anoxic conditions. At this time, the ammonia levels become very high, exceeding 50 μg-at l^{-1}. This accelerated accumulation can be explained by the high rate of ammonia production which accompanies nitrate and sulfate reduction (Richards, 1965), and also by the absence of nitrification which prior to anoxic status had been proceeding simultaneously with ammonia production. The ammonia levels during the spring of

1966 appeared considerably higher than those reached in 1964. However, this may have been an artifact due to the analytical method used during 1966. The isotope-dilution technique using nitrogen-15 labeled ammonia seems to give higher results than the sodium phenate method used on the earlier samples. Fluctuations in the rather low summer ammonia levels probably result from variations in plant activity.

Nitrite has not been included in the table, because it was only present in very low amounts at all times. The concentrations ranged from 0.03 μg-at l^{-1} to 0.35 μg-at l^{-1}, with a mean of less than 0.1 μg-at l^{-1}. This is consistent with the tendency for rapid transition between ammonia, nitrate and molecular nitrogen which is shown by the ammonia and nitrate information. Nitrite, under such conditions has a very short residence time in the water.

Phosphorus

The annual behaviour of the reactive phosphorus was similar in general pattern to the other nutrients. Accumulation under the ice in winter resulted in a maximum early in May, with almost complete removal again by mid June. This removal was without question biological, since the timing of the major change in phosphorus concentration coincided with major periods of phytoplankton production. During the summer, a low concentration was maintained, ranging between 0.2 and 0.6 μg-at l^{-1}. The linear character of the fall increase suggested that the rate of phosphorus regeneration was constant.

Dissolved organic phosphorus was determined only during a rather short time-span between February and July 1964. During this time, minimum values of 0.5 μg-at l^{-1} were found at all depths during the later summer determinations, whereas the maximum value of 10.1 μg-at l^{-1} was found in the 2 meter water following the May algae pulse. Relatively higher values were also found during the June bloom. In the case of particulate phosphorus, the maximum during the bloom was even more spectacular; during this time 14.2 μg-at l^{-1} were found in the surface water. In general, however, the particulate phosphorus concentrations were not particularly high, and with the exception of the example just cited, ranged between 0 and 3 μg-at l^{-1}.

Silicate

In waters populated with a diatom-dominated flora, silicate silicon often acts as limiting factor. Although diatoms do not form the major component of the Smith Lake phytoplankton biomass, during the spring of 1964, the silicate concentration had dropped from 48.7 μg-at l^{-1} on 18 May to 1.9 μg-at l^{-1} by 25 June. The levels remained close to the latter figure during the summer. During the 1966 spring, there appeared to be a similar drop in concentration which was, however, followed by a rather rapid restoration of higher concentrations during the summer.

Quite clearly, the distribution of nutrient compounds in Smith Lake water is largely biologically controlled, with income from the watershed playing a rather reduced role. The concentration of nutrients in the incoming water during the brief melting period is not high, and this supply is quite temporary. For both ammonia and phosphate, high concentrations were found on 5 May 1964, but on subsequent dates the concentrations were less. The single determination for silicate in inflow water does indicate that significant amounts of silicate were present in run-off water.

D. Trace metals

Results of the determinations of the total quantities of copper, manganese, and zinc are shown graphically in Fig. 11, and a summary of the results appears in Table 8. Sampling for total concentrations of these metals and for dissolved iron and manganese was done *ca.* 16 times at each of two or three depths from 31 May 1964 through 9 November 1966. Analyses for total cobalt are reported from 21 July through 9 November 1966.

The concentrations of iron and manganese in Smith Lake undergo a well-developed seasonal cycle, with iron usually being *ca.* ten fold more abundant than manganese. The summer surface values for total iron are just over 100 μg l^{-1}, and for total manganese somewhat below 10 μg l^{-1}. Large increases occur under the ice during the winter, with iron concentrations exceeding 600 μg l^{-1} by April. During the winter the manganese concentrations of the water increased to more than 90 μg l^{-1} in 1964 and to more than 50 μg l^{-1} in 1966. In 1964 iron and manganese concentrations decreased during June as mixing gradually destroyed the pronounced chemical stratification which had persisted through the spring break-up. In 1966 the drop in iron and manganese concentrations from winter levels occurred earlier in the year, coinciding with the melting of the ice cover. Both metals increase at 2 m during the summer, but the 0 and 2 m values tend to converge by August. Manganese and iron concentrations obviously respond to changes in redox conditions in the lake; but, since the iron values in the lake water increase substantially even while several $\mu g\ l^{-1}$ of dissolved oxygen remain, it seems likely that the oxidation-reduction environment at the sediment surface, rather than in the water column, is a particularly important factor in the chemistry of these metals in Smith Lake. Dissolved iron, i.e. that passing through a 0.5 μ filter, is much more abundant than particulate iron and usually amounts to more than 90% of the total iron at a depth of 2 m. Dissolved forms of manganese also are abundant, but relatively higher concentrations of particulate manganese occur in the water, particularly during the spring circulation.

The copper concentration in Smith Lake is low, in general less than 4 $\mu g\ l^{-1}$, and no seasonal cycles or consistent variations with depth are evident. Zinc, like copper, is usually present in low abundance, but an exceptional hypolymnic enrichment similar to that noted for iron and manganese is evident from the early 1964 data. In the 1966 data there is a positive correlation between the short term variations in copper and zinc, but the changes in the concentrations of these metals do not correspond well with other chemical parameters. The mean cobalt concentration in the lake was 1.1 $\mu g\ l^{-1}$ on 21 July 1966 and decreased steadily to 0.7 $\mu g\ l^{-1}$ on 6 October, then increasing to 0.9 $\mu g\ l^{-1}$ on 9 November. During this limited period cobalt, iron, and manganese follow identical patterns of variation.

Determinations for molybdenum have been made on water from Smith Lake taken from 0.6 and 2.0 m on 7 November 1967. The molybdenum concentration in both of these samples was 0.2 $\mu g\ l^{-1}$. Preliminary results of further analyses for molybdenum indicate that similar low molybdenum concentrations are present in the summer.

The ability of organic acids to hold iron in the water column under oxidizing conditions is comparatively well studied (Shapiro, 1964), and this phenomenon is apparent here. In Smith Lake copper, lead, and zinc are firmly bound by organic constituents, and in the case of lead the apparent stability constant for lead-organic complexes recovered from the lake exceeded 10^{20} (Barsdate and Matson, 1966). Recent work on a number of high-latitude lakes including Smith Lake indicates that cobalt and manganese also are bound by organic material and confirms the previous observation that molecular weight of the organo-metallic complexes is greater than 1000 (Barsdate, 1970).

E. Bottom deposits

The sediments of Smith Lake are fine-grained and organic-rich, and even in the littoral zone sand-size and larger inorganic particulates are rare. To a water depth of *ca.* 1 m the sediments are a dark brown *dy* characteristic of bog lakes; under the deeper waters of the lake the sediment grades into a finely divided, almost flocculent material which is grey to black in color and smells of H_2S. In three cores taken within a few meters of one another near the center of the lake in a water depth of 2.5 m, the grey to black, highly-reduced lacustrine sediments extend only to a depth of *ca.* 10 cm below the present lake bottom. At this depth a transition occurs in which gastropod shells and aquatic insect cases are mixed with *Sphagnum* and woody terrestrial plant tissue. Below a core depth of 13.5 cm the sediments consist of birch bark, wood and other terrestrial plant fragments in a matrix of peaty material. The brown color of this horizon suggests that it is fairly well oxidized.

The analyses of the sediments are presented in Table 9. The results are reported for a 21.3 cm core from the center of the lake and for a series of nine shallow (5 cm) cores taken at *ca.* 60 m intervals across the lake at water depths between 1.8 and 3.4 m. In the long core the range of concentrations for each of the transition elements (Co, Cu, Fe, Mn, and Zn) is rather small, being less than 50% of the mean for Co, Fe, and Mn and *ca.* 100% for Cu and Zn. The pattern of variation seems quite clear, with a slight depletion at the sediment surface, somewhat higher quantities of all metals in the terrestrial material, and maxima for Co, Fe, and Mn near the interface of the oxidized and reduced zones. Unlike the transition metals, P was highest at the sediment surface and somewhat lower in the deeper sediments.

VI. SEASONAL VARIATIONS IN PLANT PIGMENTS AND PARTICULATE NITROGEN

Both chlorophyll and particulate nitrogen were determined regularly to serve as parameters of phytoplankton biomass. Generally, zooplankton were excluded from the particulate nitrogen measurements, so that the large part of the values represent the active phytoplankton population.

The annual variations in chlorophyll *a* content of Smith Lake surface water are shown for 1963 and 1964 in Figures 12 and 13. In Figure 12, the particulate nitrogen values are shown in addition. Here the close correlation between the two is apparent, with the particulate nitrogen:chlorophyll *a* ratio remaining *ca.* 10 at all times except in November, when there was an increase in the particulate nitrogen:chlorophyll *a* ratio. This increase was the result of a simultaneous increase in particulate nitrogen and a decrease in chlorophyll. Particulate nitrogen levels remain at the 50 μg l^{-1} level during most of the winter, suggesting that this is perhaps a background detrital nitrogen level. The really spectacular increases are restricted to the May and June major phytoplankton production periods (see discussion below). When the several depths are plotted simultaneously (Figure 14), the time sequence becomes somewhat less clear, since the maxima at different depths do not coincide in timing. The May nitrogen peak was much higher at 2 m depth than in the water immediately under the ice, although it appeared to initiate closer to the surface. Similarly, the June peak reached a maximum at the 1 and 2 m depths earlier than at the surface. The increase at the end of August was not apparent at the surface.

VII. PRIMARY PRODUCTIVITY

A. Phytoplankton

The annual cycle

The phytoplankton primary productivity in Smith Lake underwent pronounced seasonal fluctuations, with high rates of photosynthesis occurring only in spring and early summer. During 1963, work had not begun sufficiently early in the year to observe the first productivity peak, which was detected under considerable ice-cover in May, 1964 (Fig. 15). A maximum carbon fixation rate approaching 28 μg C l^{-1} hr^{-1} was measured during this peak, which has already been briefly mentioned above in connection with its probable role in terminating the anoxic condition of the water. This first period of intensive production was, however, over before the lake became ice-free. The decline was probably a result of the drastic reduction in nutrient content which took place during this production period. For example, the entire ammonia content accumulated during the winter had been reduced to undetectable levels.

The highest rates of primary production of the entire annual cycle were consistently found in June, shortly after the lake had become ice-free. Each year the population of algae responsible were strikingly dominated by *Anabaena flos-aquae* and the timing of the bloom was very consistent during the years observed. The rate of increase in photosynthetic rate was similar during 1963 and 1964, and the peak was attained on the same day during both years (Fig. 15 and 16). The rate of post-bloom decline was much more rapid during the second year, and the maximum photosynthetic rates observed (90 μg C l^{-1} hr^{-1}, *in situ*) was considerably lower than the maximum of 175 μg C l^{-1} hr^{-1} measured in 1963. Thus conditions were apparently less favorable in 1964, resulting in the lower production and more rapid decline. There is reason to believe that the stability of the water column was a determining factor. The temperature, alkalinity, and dissolved solids depth curves indicate that both chemical and thermal stratification were established as the ice melted in 1964, and remained during the entire month of June (Figures 3, 7 and 8). In 1963 the lake had mixed more completely upon melting. The availability of nutrients in the surface water can be strongly influenced by such mixing, since the absence of circulation causes the dilute ice-melt water to form the epilimnion and remain in the surface region.

Following the decline of the *Anabaena* population, relatively lower levels of productivity continued during the summer, with minor fluctuations. The few primary productivity experiments which were carried out in 1966 and 1967 were confined to the June period, and were done in order to monitor the bloom. Many of the incubations were carried out in the laboratory. The results (Tables 10 and 11) confirmed the findings of the previous years. In the 1967 series, the light *in situ* bottle was lost on 12 June, and this may have been the peak photosynthesis day for the surface water. Therefore, little can be said about the relative production compared with the other years, except that the rates of photosynthesis appeared to be somewhat lower in 1967 than in 1966 under similar incubation conditions. Again, the timing of the bloom seemed to be reproducible annually, whereas the rates of production and total production varied considerably between seasons.

Comparative in situ and in vitro incubations

During May 1964, the peak productivity rate measured under constant temperature and light incubation was 33.5 μg C l^{-1} hr^{-1}, compared with an *in situ* value of 28 μg C l^{-1} hr^{-1}. This difference suggests that perhaps the production under the ice was light limited at its peak, or that temperature may have had an effect. Lake water incubated at 20°C under illumination with HVO gro-lux lights showed a peak one week earlier than the *in situ* samples, again suggesting a potentially higher photosynthetic rate *in situ* which was limited by light or temperature. The June peaks coincide in time regardless of incubation method. During 1964, incubations carried out at constant temperature showed a trend towards a fall rate increase which did not show up in the *in situ* samples, again suggesting *in situ* limiting conditions (Fig. 17).

Photosynthesis and depth relationships

In addition to plotting surface primary productivity rates, the 1963 results of *in situ* incubations have been expressed in terms of carbon fixed under a square meter surface area per hour, by integrating depth-photosynthesis curves for each experiment. This treatment produces an annual cycle which shows the major June peak rather dramatically (Fig. 16). In the same figure, the values for carbon fixation rates in the surface water expressed in terms of unit water volume would suggest higher total rates for the entire water column. The low total is due to the high extinction coefficient caused by the water color and light absorption by the phytoplankton in the water column. Thus, especially during the production maximum, high photosynthetic rates tend to remain confined to the surface layer. Selected depth-photosynthesis curves illustrate the vertical distribution of photosynthesis in Smith Lake (Fig. 18). The euphotic zone in Smith Lake is very restricted, and the 1% light level seldom reaches 2 meters. There are some seasonal variations, with minimal penetration in June, September and October and with clearest water in mid-summer. Light penetration has been discussed in a previous section.

The relationship between chlorophyll a and photosynthesis

The photosynthetic rate of carbon uptake on a unit chlorophyll *a* concentration basis may be used as a measure of the photosynthetic efficiency of the chlorophyll under the particular environmental and physiological conditions encountered. Among factors which affect the assimilation number thus obtained are light and the availability of nutrients. Previously, low photosynthetic activity of chlorophyll was found under reduced light conditions in ice-covered lakes (Saijo and Sakamoto, 1964). This low activity was not only due to the low light *in situ*, since the maximum photosynthetic rate obtained under saturation light intensities remained low for these shade-adapated organisms. The photosynthetic efficiency of the chlorophyll *in situ* in Smith Lake proved surprisingly high, in spite of a considerably thicker ice-cover than was encountered in the Japanese lakes cited above. *In situ* primary productivity results have been tabulated with chlorophyll *a* concentrations, and with the assimilation number obtained here, under 0.7 m of ice in May, correspond to those frequently found in eutrophic lakes under optimal conditions. Ichimura and Aruga (1964) suggest 2 to 6 mg C per mg Chl *a* hr^{-1} as typical for eutrophic waters. In addition to the already high values *in situ* in Smith Lake, the assimilation number could be increased by incubating at higher light intensities in the laboratory, again contrary to the behavior of a shade-adapted population, in which a low saturated photosynthetic rate would be expected.

Although Saijo and Sakamoto (1964) suggest both heterotrophy and a long generation time at low temperatures as mechanisms which may allow the growth of a considerable algae population under ice, in Smith Lake the photosynthetic rates alone appear adequate to explain the growth of the populations at all times. The possible importance of a reduced respiration rate at the relatively low temperatures in allowing high net photosynthesis is not established.

Primary productivity in winter

In situ work is not practical during much of the Alaskan winter, and as a result, much of the winter work has involved incubation at 5°C and under low light intensities in the laboratory. Such experiments have shown a comparatively high rate of carbon uptake, but comparison of the results of light and dark incubations indicate that most of this uptake is not light-related, and therefore not photosynthetic (Table 13). The water immediately above the mud surface showed especially high carbon uptake rates, suggesting that such uptake is heterotrophic, the result of a healthy microbial population. On 25 May, a clearly photosynthetic production was evident in the bottom water.

The structure of the ice does not remain constant during the winter, and especially during the spring there is a tendency for overflows of water over the ice, with subsequent refreezing. An experiment was carried out to test the primary productivity within the snow cover, the overflow water, the various ice layers and the lake water itself at two depths. Incubations were done in the laboratory, and in order to carry out the primary productivity measurements, the ice and snow sections were allowed to thaw. The results are shown in Table 14, with chlorophyll *a*, nutrient distribution and water color within the various layers. Highest rates of photosynthesis were measured in the top layer of overflow ice, and low, but positive rates were found in the snow layer and in the lake water immediately below the ice. No chlorophyll was found, nor was photosynthesis detected in the second overflow ice section or in the clear ice immediately adjacent to the water.

B. Epiphytes

Although epiphytic algae can be seen on suitable substrates in the lake during the entire ice-free season, they are most prominent in late summer and autumn, when they are abundant on the stems and lower leaves of benthic plants (particularly *Potamogeton*) and on the detrital accumulation which forms along the margins of the lake from emergent plants.

In order to assess the contribution of epiphytes in relation to the productivity of the plankton algae and macrophytes, a vertical series of microscope slides was suspended in the lake on 29 June 1965, and the accumulated organisms harvested after periods of 14 and 30 days. Chlorophyll *a* and particulate carbon determinations were done on the samples; the results appear in Fig. 19. The decrease in carbon: chlorophyll *a* ratios from the surface to a depth of 1 m presumably is the result of shade adaptation with reduced light levels; below 1 m the carbon:chlorophyll *a* ratio is higher due to the occurrence of animal components of the *Aufwuchs*. The large increase in biomass of the 30-day samples over the 14-day samples is not due to more favorable conditions of light, temperature, or nutrients, as a similar series of slides suspended for 16 days from the date of termination of the 14-day experiment to the end of the 30-day experiment was only slightly higher in carbon and chlorophyll than the 14-day values. Some time lag is involved before organisms become established on a new substrate and presumably the growth of epiphytic algae is somewhat logarithmic in nature. These factors, rather than conditions more favorable to rapid growth, are responsible for the much larger accumulation in 30 days.

The amount of substrate cannot be estimated to a useful degree without more field work than has been applied to the problem, and consequently it is not possible to estimate the productivity of the epiphytes under a unit area of lake surface. However, the average daily rate of carbon accumulation on glass substrates for the 30-day experiment was more than 2 μg C cm^{-2} day^{-1}, and by mid-September the accumulated biomass on natural substrates near the lake margin amounted to several hundred μg cm^{-2}.

C. Macrophytes

Mean values for the standing crop of rooted vegetation were derived from samples taken at six transects around the lake during the period from 20 July to 30 July 1964. Vegetation was most dense at depths of 0.5 to 1.0 m (Table 15). Probably because of the extreme light attenuation, the plant abundance dropped off rapidly with depth, and at 2 m the flora consisted largely of water lilies (*Nuphar* sp.).

During the early part of the ice-free season there is little rooted vegetation in the lake, and, considering the high rates of planktonic primary production which occur during the spring bloom, macrophyte productivity is relatively less important than later in the season. The standing stock of benthic plants is well developed by late July and seems to increase at a reduced rate through August. Much of the material remains in place during September but is not growing actively and often is covered by a luxurious growth of epiphytes.

To compare the productivity of the benthic plant community with that of the phytoplankton, oxygen evolution measurements were made on samples of the five most abundant benthic species. These data represent close to the maximum rates likely to occur in the lake, as they were done with healthy-looking, vigorously-growing samples incubated for a short time under nearly optimal light conditions. Photosynthetic carbon fixation was estimated using the assumption that the evolution of 32 g of oxygen results in the fixation of 12 g carbon. If the further assumption is made that the rate of plant tissue accumulation is 2.5 times the rate of carbon fixation, extrapolation of the carbon values in Table 15 would indicate that the plant material was accumulating at a rate of approximately 0.4% per hour. If allowances are made for the presence of less actively growing portions of the plants discriminated against in sampling, for reduced light intensities from shading and depth, and for respiration during the relatively short nights, this figure would be somewhat lower. However, it appears that in terms of net rate of carbon fixation per unit lake surface area, benthic productivity exceeds phytoplankton productivity during the summer months.

VIII. PHYTOPLANKTON

The several years of qualitative observations on the algal populations in Smith Lake have been combined to give an indication of the grossly obvious variations in composition which accompanied the seasonal variations in productivity. Quantitative data were not generally obtained, and quite possibly the rarer components of the flora were often missed.

During the winter months, the number of algae in the lake was always very low, and in the majority of water samples nothing at all could be detected. For instance, although in February, an occasional *Chlamydomonas* sp. or a μ-flagellate was found, most water samples contained only detritus. This was also the case during March. We were interested to find large numbers of zooplankton in the lake mud during March, although none were present in the water column. By the end of March a few *Chlorella* sp. and more μ-flagellates were present, and early in April zooplankton appeared at all depths in spite of the presence of H_2S. During April the number of individuals of *Chlorella* sp. increased, and by mid-April, *Euglena* sp., *Glenodinium* sp., and a blue-green filamentous form tentatively identified as *Nostoc* sp. were found immediately below the ice. At this time, oxygen in low concentration was once more detectable immediately below the ice. The increased algal population at this time has been suggested as a possible contributing cause for this appearance of oxygen.

As the population built up during May, many *Chlorella* sp., *Chlamydomonas* sp., *Glenodinium* sp., were found, with maximum numbers initially appearing near the mud surface. By the end of May, large numbers of *Glenodinium* sp. were found immediately below the ice, although by this time more were present near the mud surface at 3 m. *Chlorella* sp. and *Chlamydomonas* sp. were also still present near the ice-water interface, but a large amount of decaying material with green-pigmented cells attached had appeared.

At about the time that the ice melted, the total algal biomass was low. *Chlorella* sp. still tended to be numerically dominant, with *Glenodinium* sp. present, but also occasional *Pyrobotrys* sp., *Mallomonas* sp., *Ankistrodesmus* sp. However, from this time *Anabaena flos-aquae* gradually increased its numerical predominance. In 1964, filaments of *Anabaena flos-aquae* were very abundant in the surface water; yet, below 1 m only *Chlorella* sp. and colonial green forms were present. On 12 June the qualitative depth distribution of the dominant algae was:

0.0 meters	*Anabaena flos-aquae, Chlorella* sp.
1.0 meters	*Anabaena flos-aquae, Chlorella* sp., *Mallomonas* sp., *Chlamydomonas* sp.
2.0 meters	*Chlorella* sp., *Mallomonas* sp., *Scenedesmus* sp.

On 12 June 1966 there were 2.0×10^6 *Anabaena* filaments per liter in the surface water. However, shortly after this, the filaments began to clump (the timing being correlated with the rise in pH previously discussed and illustrated in Fig. 10), and akinetes became abundant both within filaments and free in the water. Although *Anabaena* was still present in the largest numbers, *Euglena* was also found as well as μ-flagellates, *Ankistrodesmus* sp., *Spirulina* sp. and *Fragilaria* sp.

During July there was a great reduction in algal numbers following the decline of the June "bloom", and there were a large number of decomposing *Anabaena* filaments in the water. At the end of July, the algae were still low in number, although several genera were observed in this small but diverse population. These included *Chlorella* sp., *Chlamydomonas* sp., *Glenodinium* sp., *Selenastrum* sp., *Scenedesmus* sp., *Ankistrodesmus* sp., *Cosmarium* sp., and *Planktosphaeria* sp.

During August, *Aphanizomenon flos-aquae* became the numerically most important alga. This species appeared in the surface water at the beginning of August, while decaying material with green pigmented cells attached still characterized the 1 and 2 meter depths. *Aphanizomenon* persisted as the dominant form during the entire month, and occasional *Anabaena* filaments were found, as well as *Selenastrum* and *Chlorella*. By September *Selenastrum* sp. and *Chlorella* sp. had become very abundant with *Askenasyella* sp. also present in considerable numbers, at first near the mud-water interface. During October, *Glenodinium* sp. had become the only form present in significant numbers. Shortly after this, winter conditions prevailed, and no algae were evident until early spring.

On the basis of the information presented above, the marked differences between the populations during the under-ice "bloom" and the June "bloom" can be seen. The general pattern seems to be the classical "bloom" characterized by a population of low diversity, and between these periods of high productivity much decaying material was present in the water, and a low but diverse population would develop. The only exception to this was the August *Aphanizomenon*-dominated community, during which, although productivity was not high, the population was highly dominated by the single species. The large number of zooplankton present may have accounted for the low productivity through heavy grazing. The most spectacular productivity peaks, although only separated by a month or less in time, were attributable to extremely different populations, the first a typical low-light, high nutrient community and the second a high-light, low-nutrient-adapted population dominated by *Anabaena flos-aquae*.

IX. SUMMARY AND DISCUSSION

Smith Lake is essentially dimictic (Hutchinson, 1957) with some distinguishing properties. In spite of the shallow water depth the spring turnover often is incomplete since low density ice-melt water, the short wind fetch during the moat formation period, low wind velocities, and very rapid heating at the surface restrict circulation. Surface temperatures exceeding 25°C and extreme temperature gradients are reached during the short period of summer stratification, and autumnal mixing which starts in August continues until freeze-up in October. The thermal regime is vastly different from that of high arctic lakes or of Alaskan coastal lakes at the latitude of Smith Lake. The former are unstratified, have a somewhat shorter ice-free period, and attain maximum temperatures of 8° to 15°C. The latter are dimictic, have a much longer ice-free period than Smith Lake but with few exceptions do not attain maximum temperatures approaching 20°C. Considering the prolonged periods of extremely low temperatures that characterize the continental subarctic winters, the Smith Lake ice accumulation (usually less than 0.8m) is surprisingly modest. Two factors seem important here; one is the high heat flux from the sediments, and the second is the persistent winter snow cover. Although this snow seldom is very deep, the wind velocities are insufficient to transport the insulating snow from the frozen lake surface.

The exclusion of salts from ice plays a role in the winter chemical regime, and in this there is a similarity with lakes and ponds of the arctic coastal plain, where freeze concentration can cause a four-fold or more variation in major components (Boyd, 1959; Kalff, 1965). In Smith Lake roughly half of the water is frozen during the winter, and the concentration of the major dissolved constituents increases approximately two-fold. The pH fluctuates around neutrality, with only a short-lived maximum due to productivity in early summer. The alkalinity is, as expected, variable with season with high values in time of drought and under the ice in winter. The annual oxygen cycle is distinguished by anoxia in late winter, accompanied by denitrification and sulfate reduction, so that hydrogen sulfide is present during the latter part of the ice-covered period. Oxygen depletion and related phenomena also occur transiently during summer stratification.

The nutrient levels appear to be biologically determined and mediated, so that high levels of combined nitrogen, phosphorus, and silica occur through regeneration after the production period and become low during the summer. The nitrogen compounds vary in a predictable manner with accumulation of ammonia and nitrate during the winter followed by depletion of nitrate through denitrification. The high organic acid content has a marked effect on transition metal chemistry, although the ecological significance is at present undefined. However, associated high water color plays an important role in the distribution of heat and light in the lakes, and both of these factors have a profound influence on the biota.

A clear succession of algal blooms as occurs in Smith Lake has not been described in other Alaskan lakes. This succession bears a great similarity to that described for lakes of Southern Saskatchewan by Hammer (1964), at least during the blue-green algae dominated period in Smith Lake. In the Saskatchewan lakes *Anabaena* populations preceeded *Aphanizomenon*, with the *Anabaena* population developing as the water temperature reaches 14° to 15°C. In Smith Lake the bloom starts to build up at similar temperatures, although here the heating rate of the surface water is so rapid that by the time the population is fully developed a considerably higher temperature has been reached. *Aphanizomenon*, according to Hammer, does not appear until the temperature has reached 20°C, which also agrees with our observations. The sharp pH rise during the June bloom may affect adversely the physiological state of the *Anabaena*, triggering the abrupt decline in the population. The strong thermal stratification restricts circulation and the advection of bicarbonate and nutrients into the surface layers. During the remainder of the summer heavy grazing may control partially the plankton productivity as zooplankton are abundant during this time.

Light is a factor that greatly limits primary productivity in Smith Lake. For over six months of the year starting in October, an extremely low light environment exists in the lake, the result of a short day length, the low solar angle, and the high albido of the snow. In the spring, as light conditions become more favorable, roughly one-quarter of the total annual phytoplankton productivity occurs under the ice. This period is characterized by the extremely high efficiency of under-ice photosynthesis, a situation apparently not observed elsewhere (cf. Saijo and Sakamoto, 1964). During the ice-free period light limitations also exist as a result of the strong attenuation of visable radiation by the colored organic acids in the water. Despite the generally favorable nutrient conditions the total annual phytoplankton production is low, approximately 11 g C m^{-2} during 1963. This is somewhat higher than the productivity of arctic lakes, which range upward to 8.4 g C m^{-2} (Kalff, 1967b), and somewhat lower than other taiga lakes (Likem and Johnson, 1968), subarctic alpine tundra lakes (Barsdate and Alexander, 1971) or Southwest Alaska coastal lakes (Hartman and Burgner, 1966).

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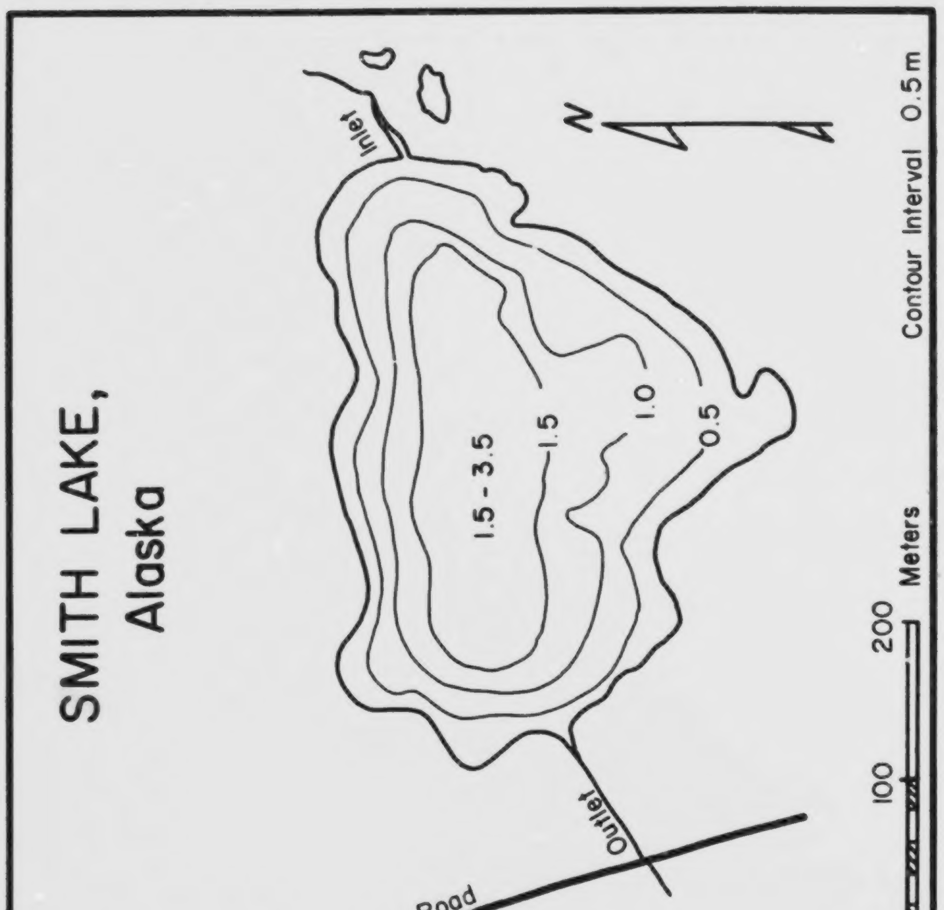
ALASKA
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Outlet
0
100
200
Meters
Contour Interval 0.5m

Figure 1. Geographical location of study area and map of Smith Lake.

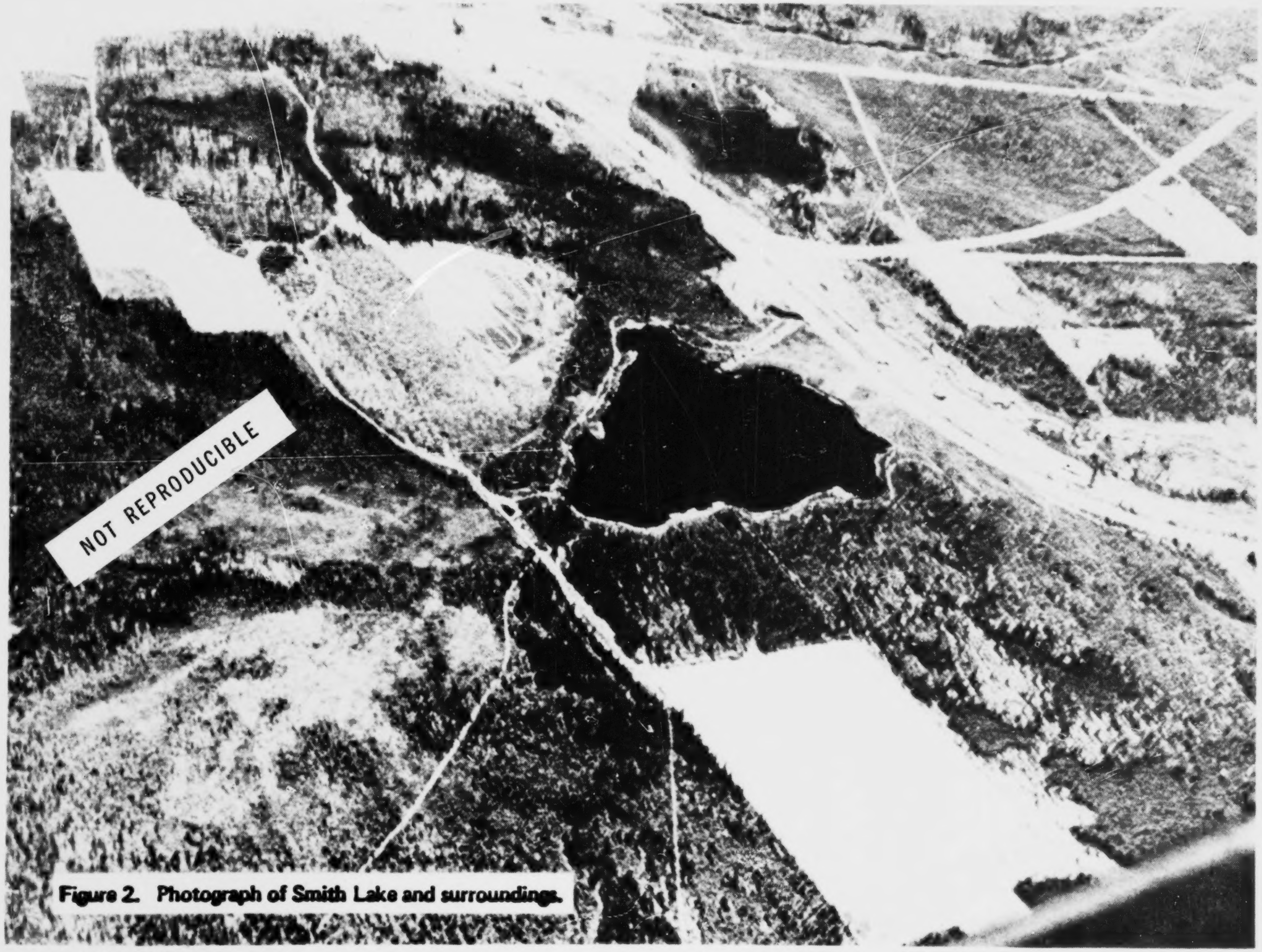

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Figure 2. Photograph of Smith Lake and surroundings.

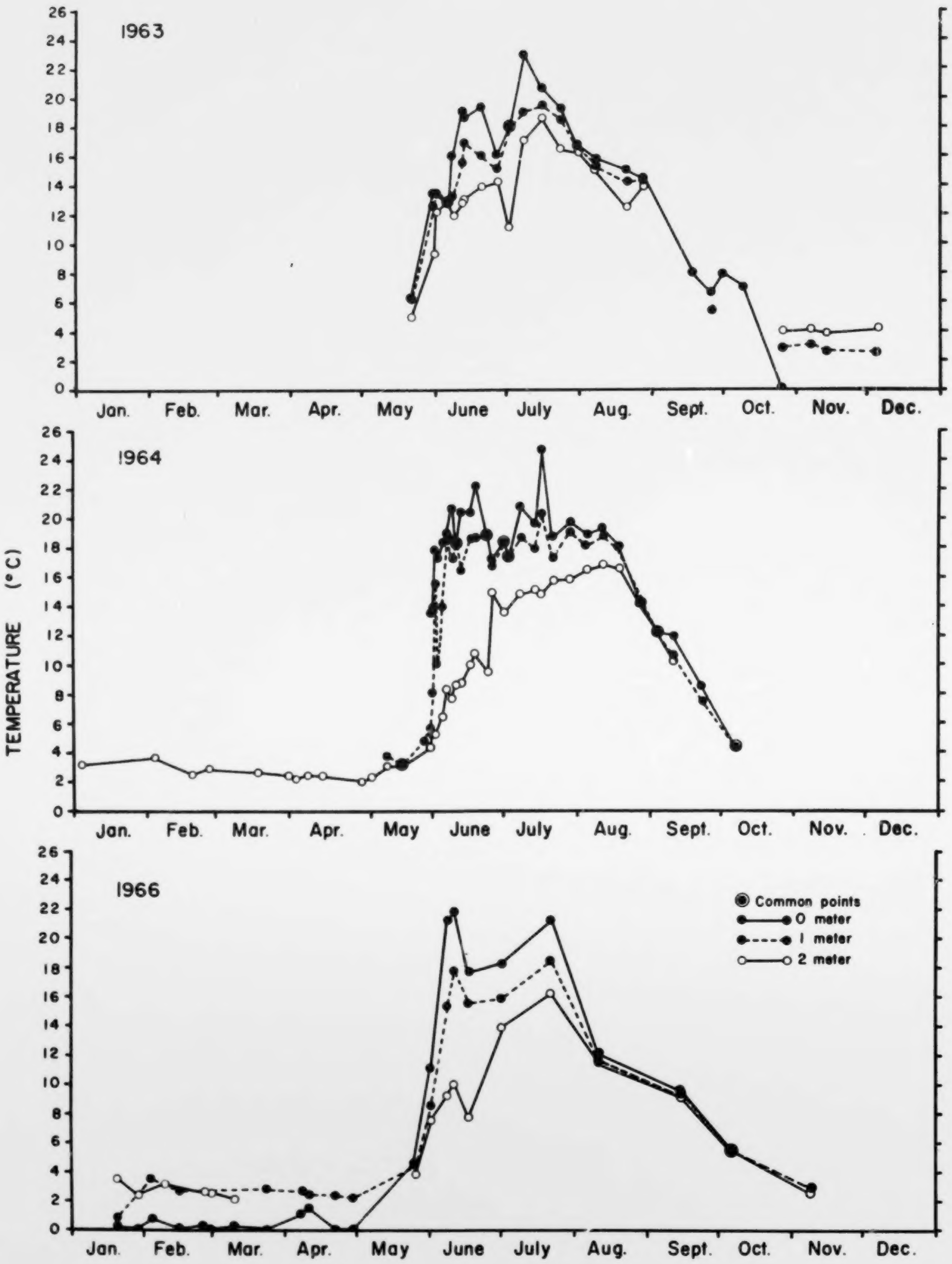

Figure 3. Seasonal temperatures - Smith Lake, 0, 1, 2 meter.

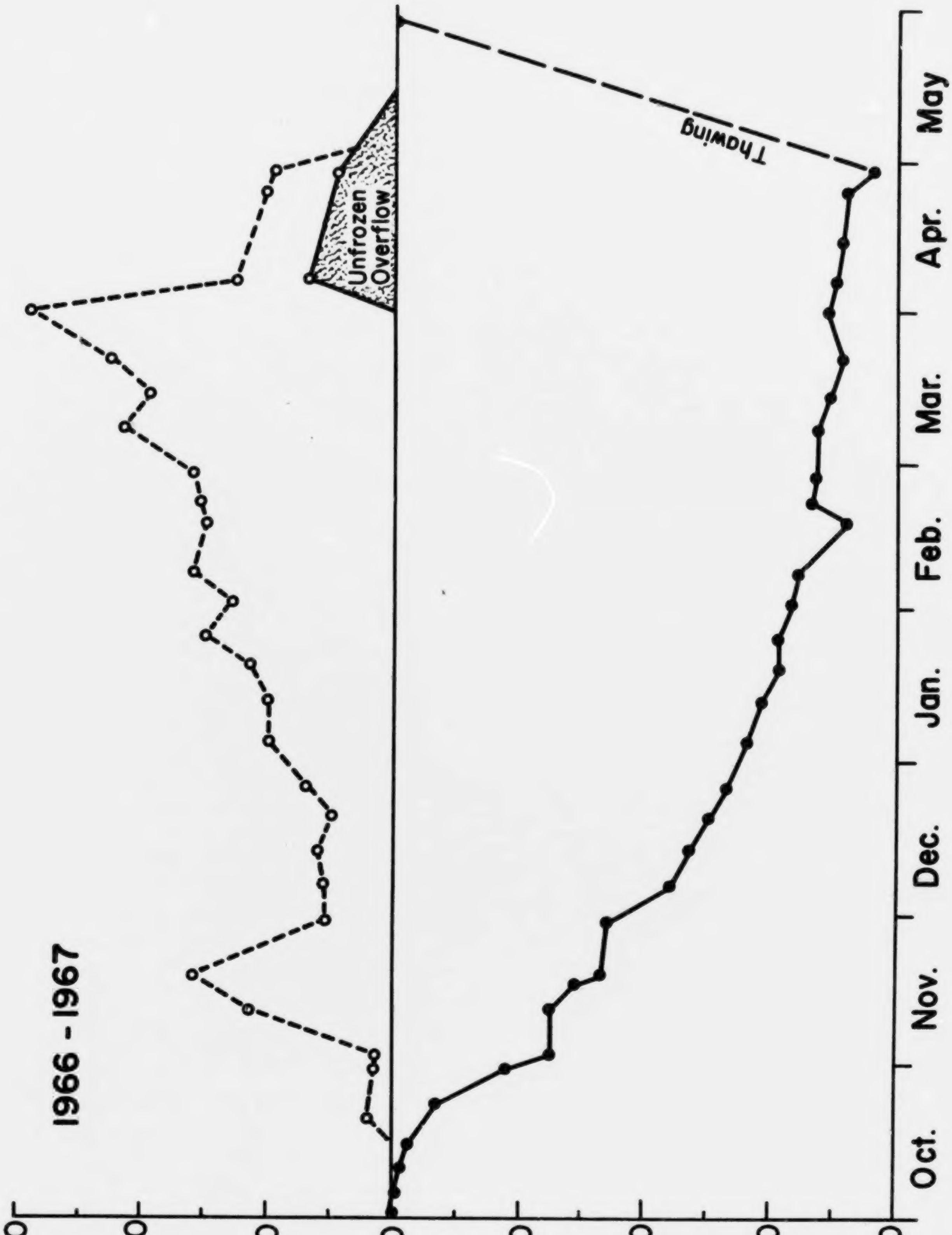

Figure 4. Ice and snow thickness.

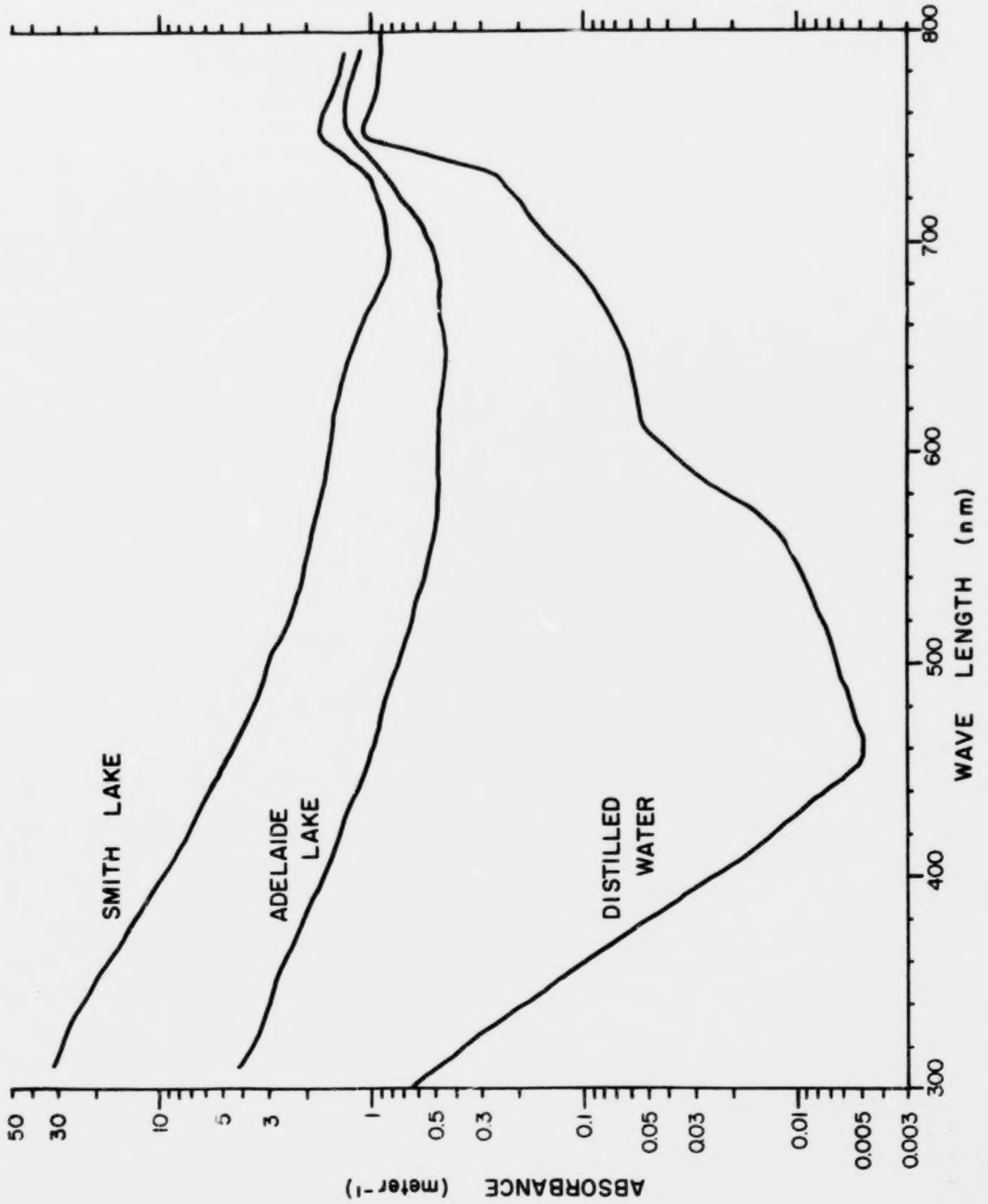

Figure 5. Absorbance of light in 1 m columns of water.

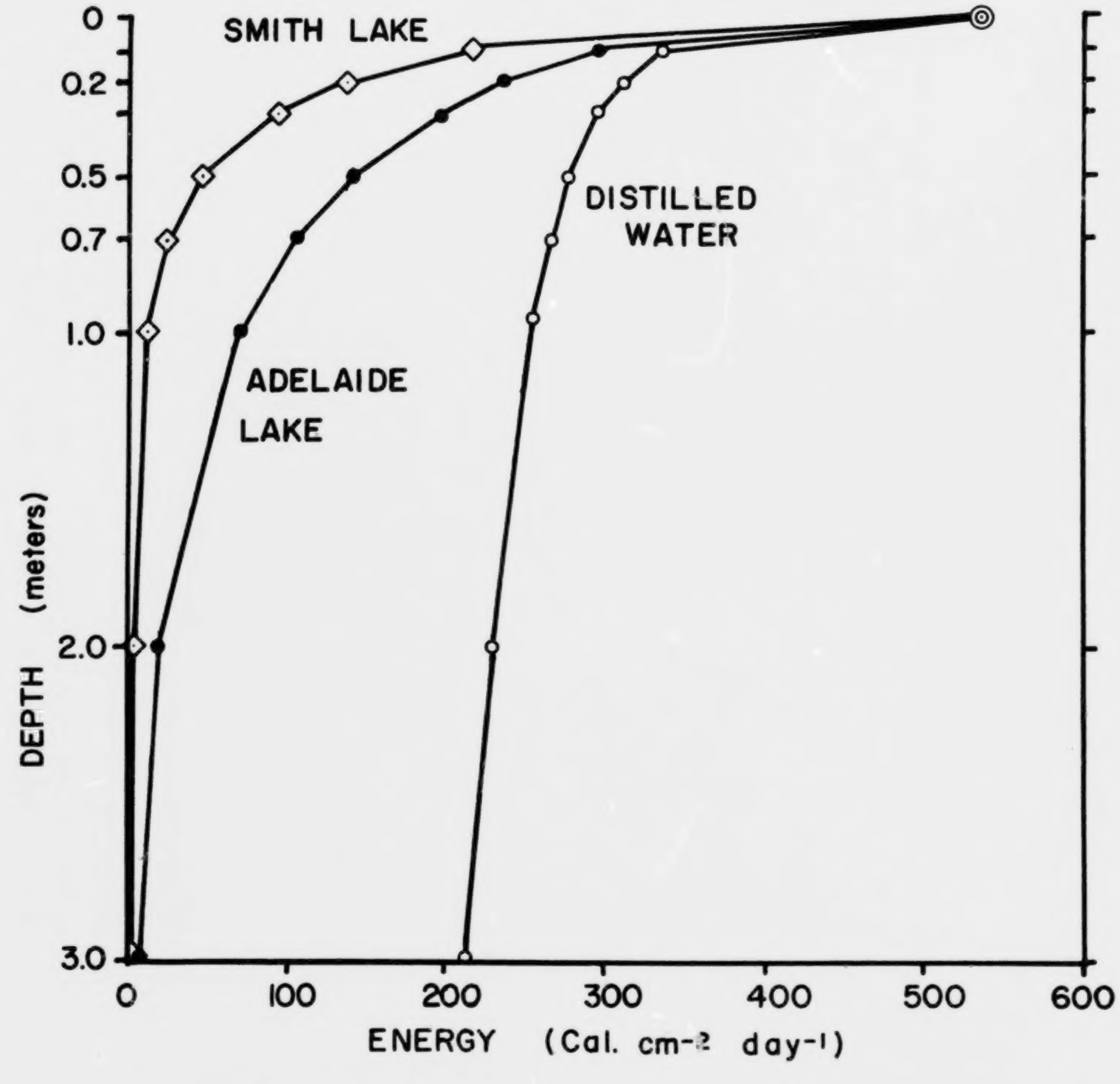

Figure 6. Transmission of solar energy to various depths for 3 water types.

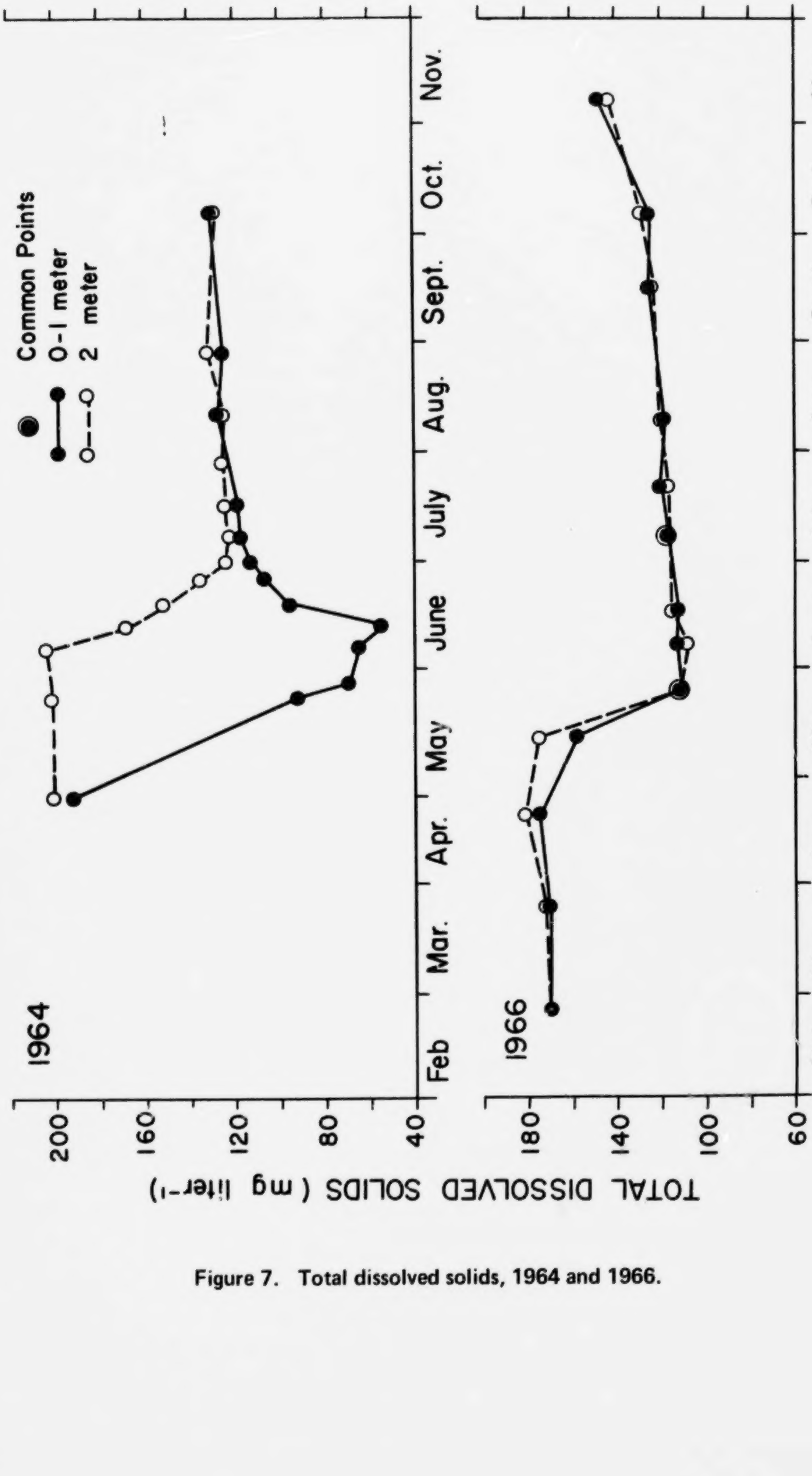

Figure 7. Total dissolved solids, 1964 and 1966.

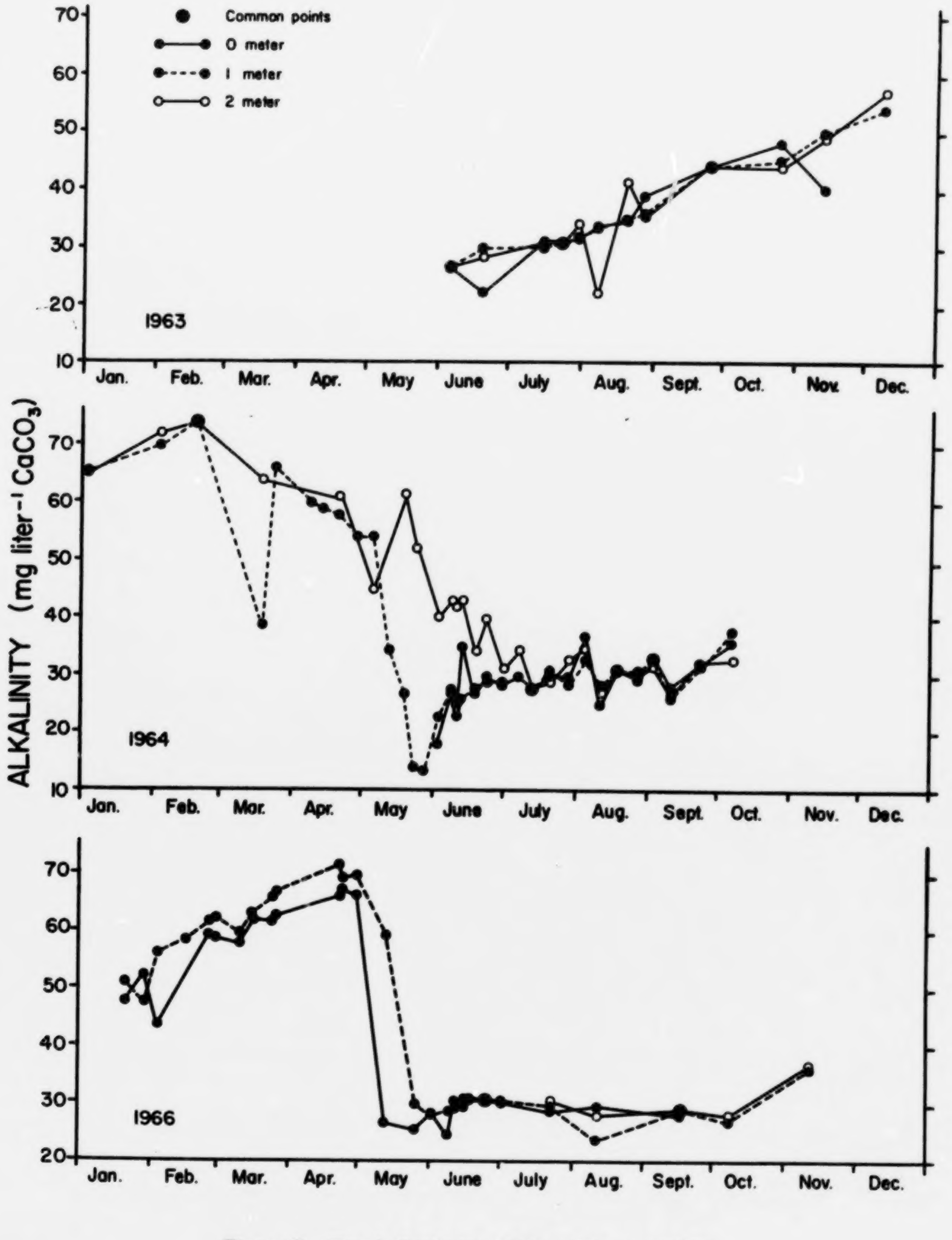

Figure 8. Total alkalinity, 1963, 1964 and 1966.

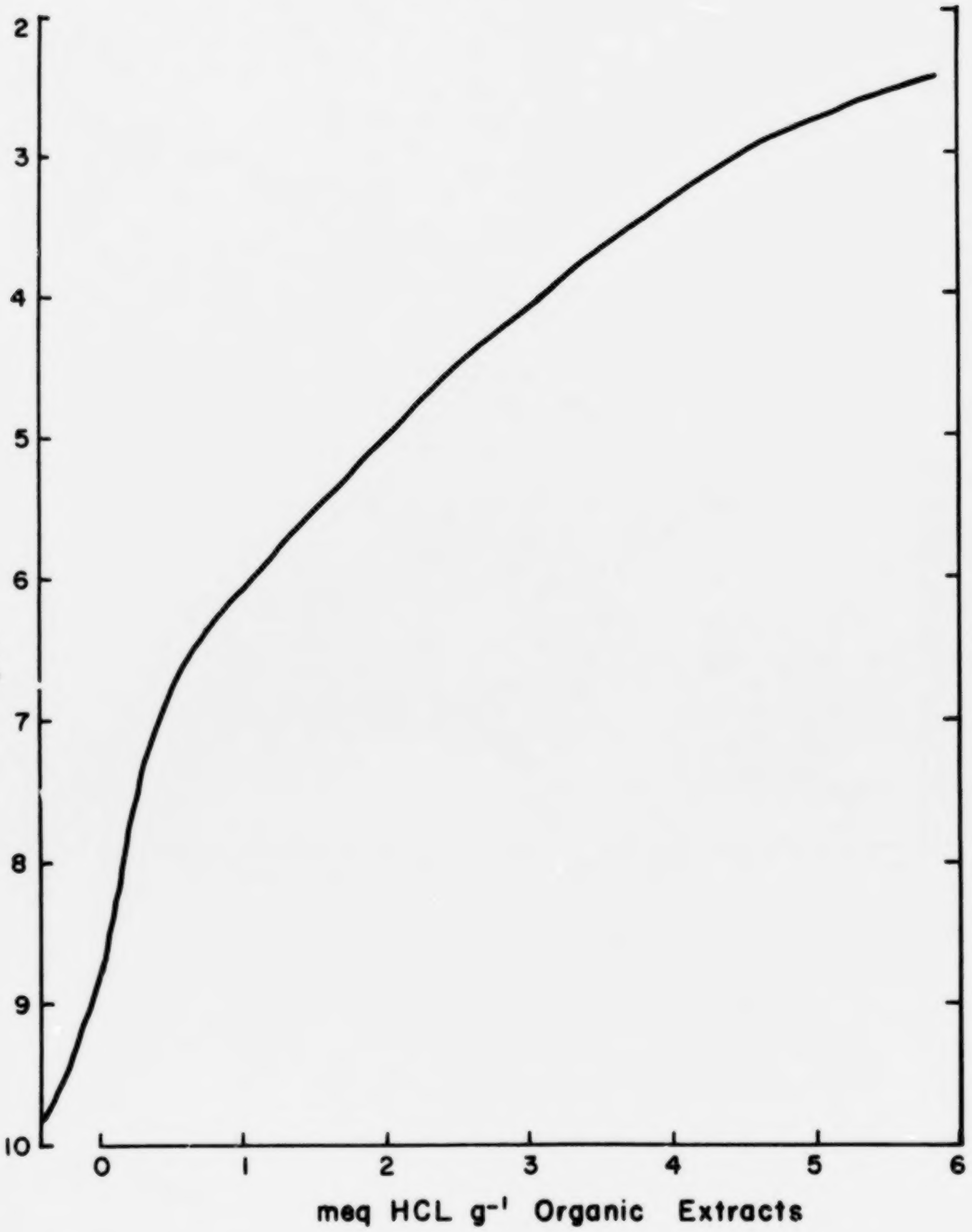

Figure 9. Titration curve for dissolved organic matter from Smith Lake.

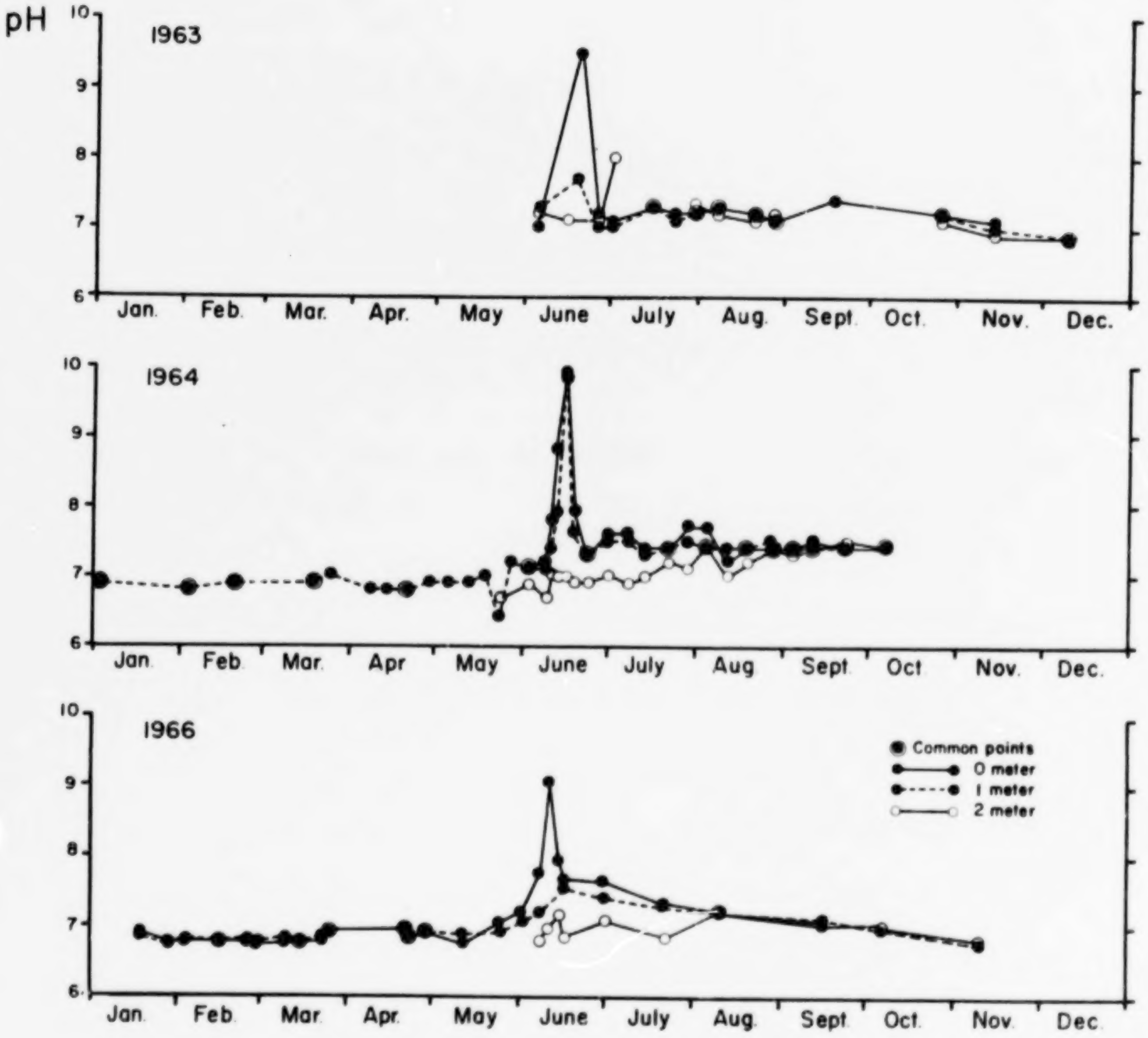

Figure 10. pH, 1963, 1964 and 1966.

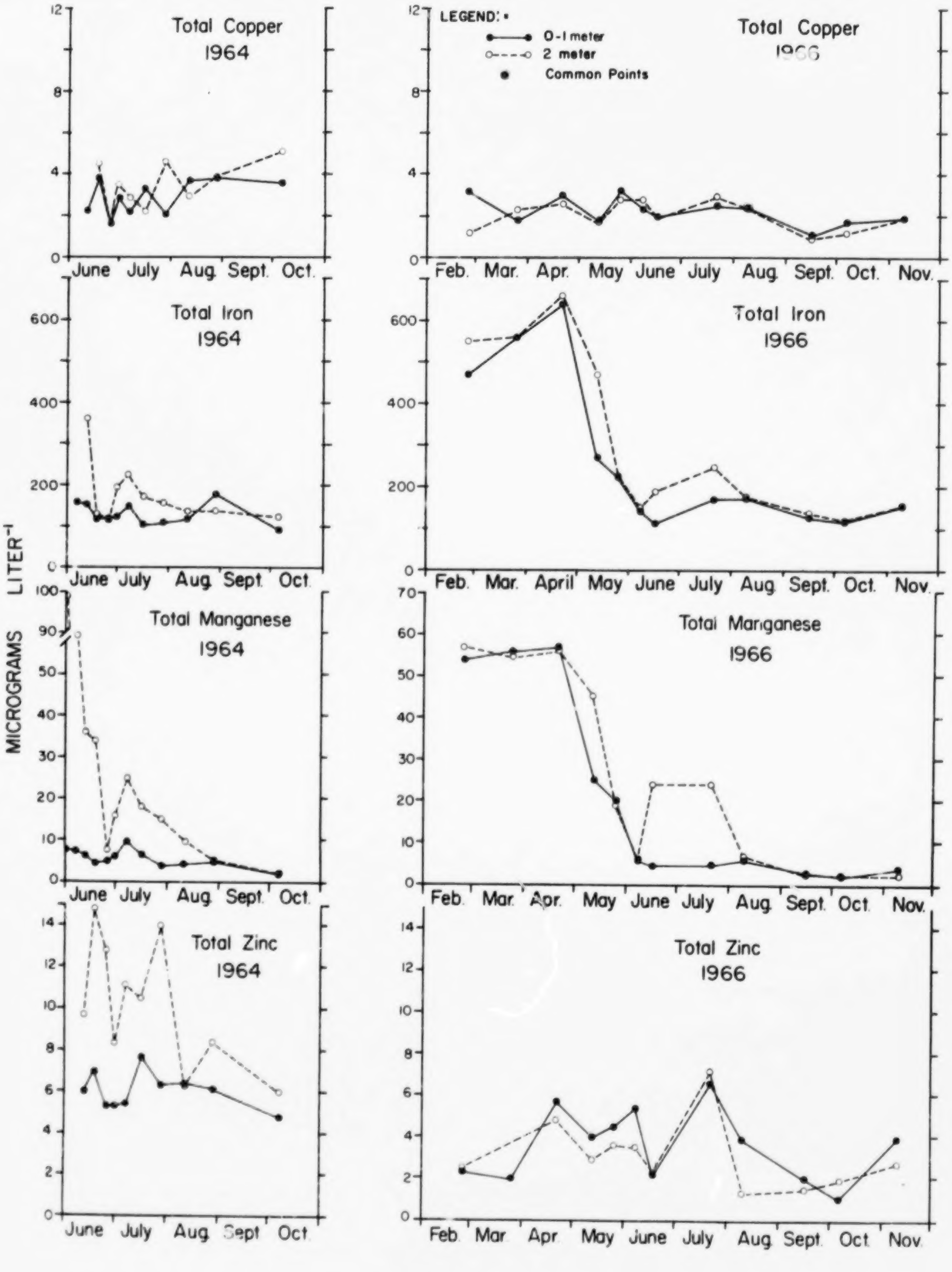

Figure 11. Trace metals.

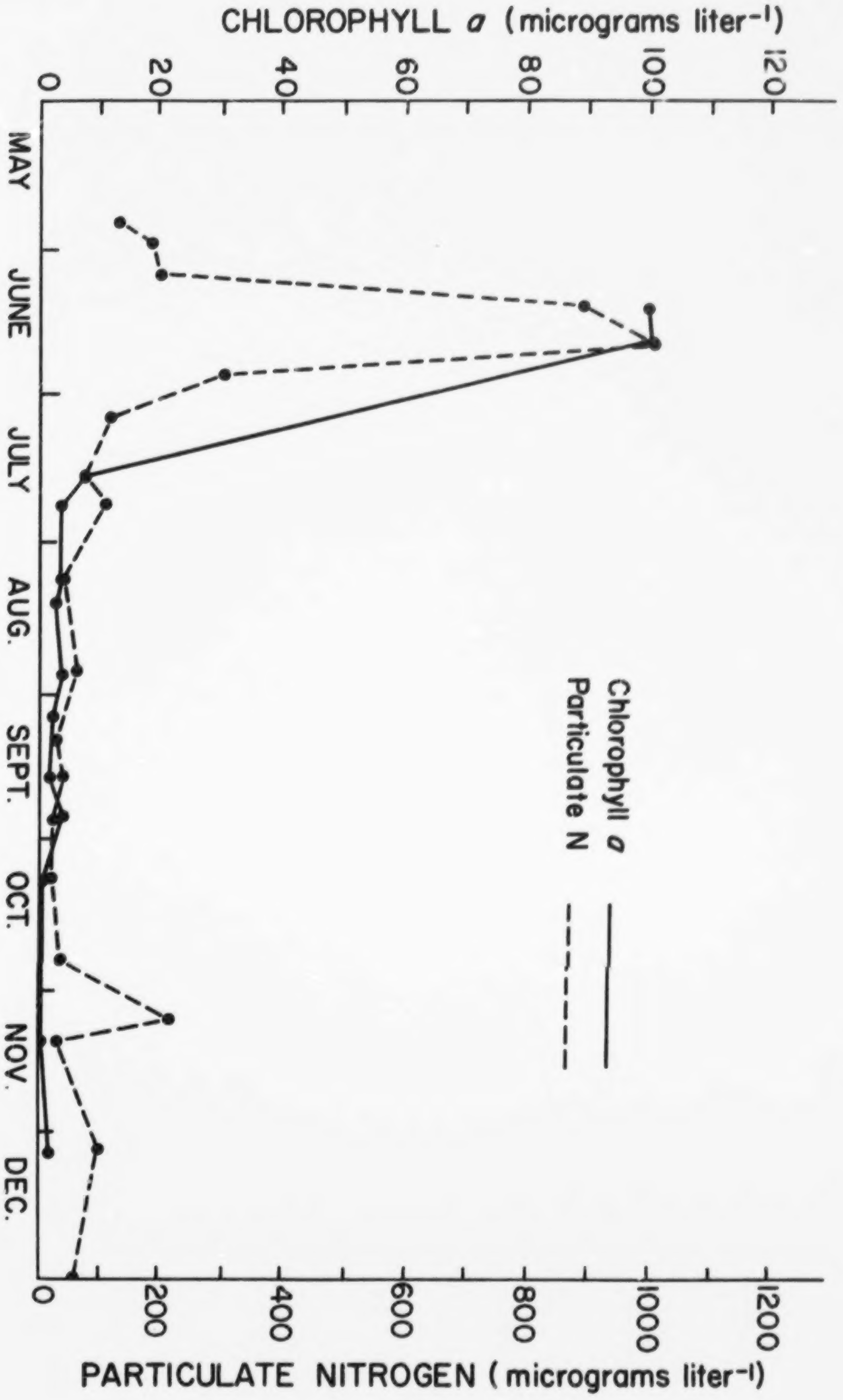

Figure 12. Chlorophyll α and particulate N, 1963.

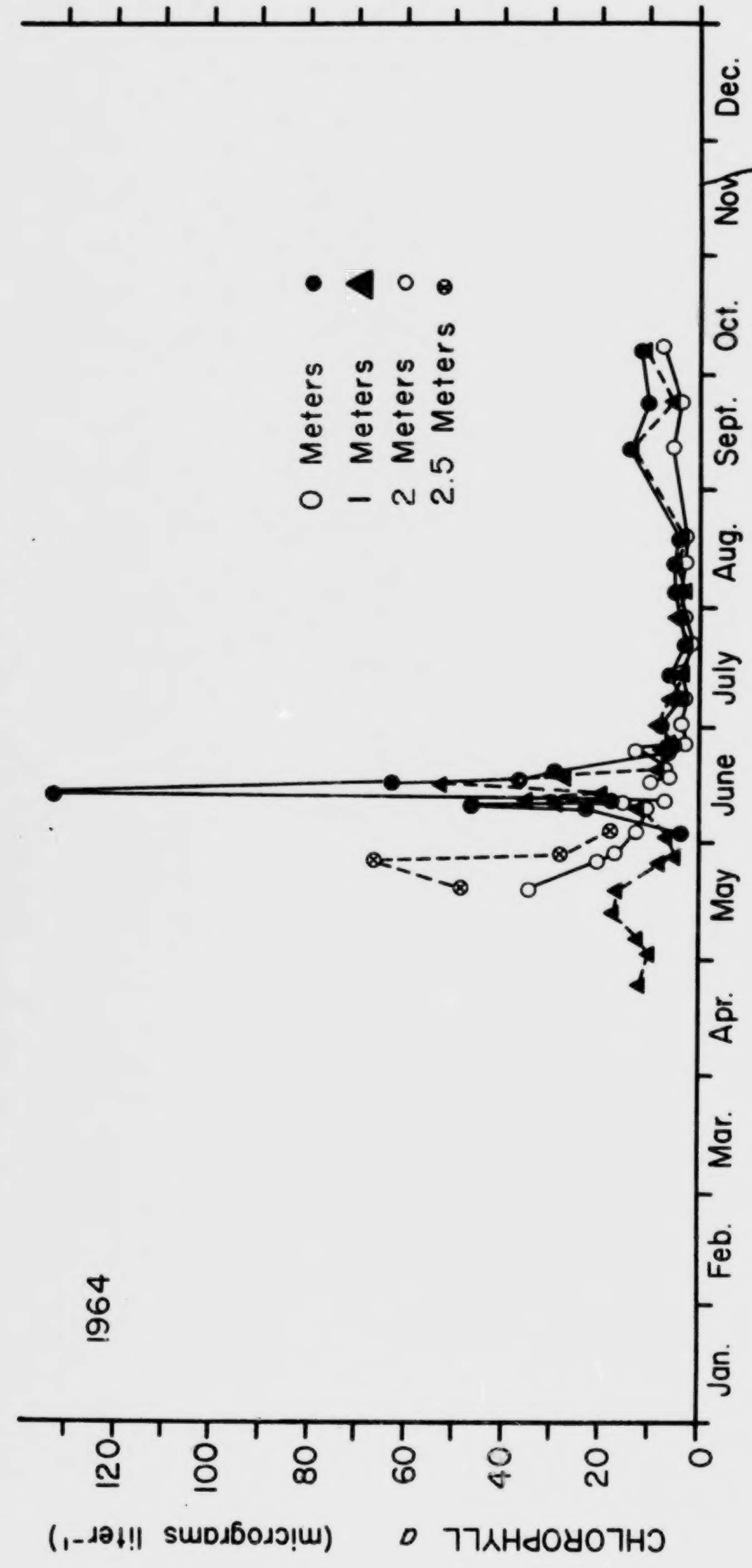

Figure 13. Chlorophyll α 1964.

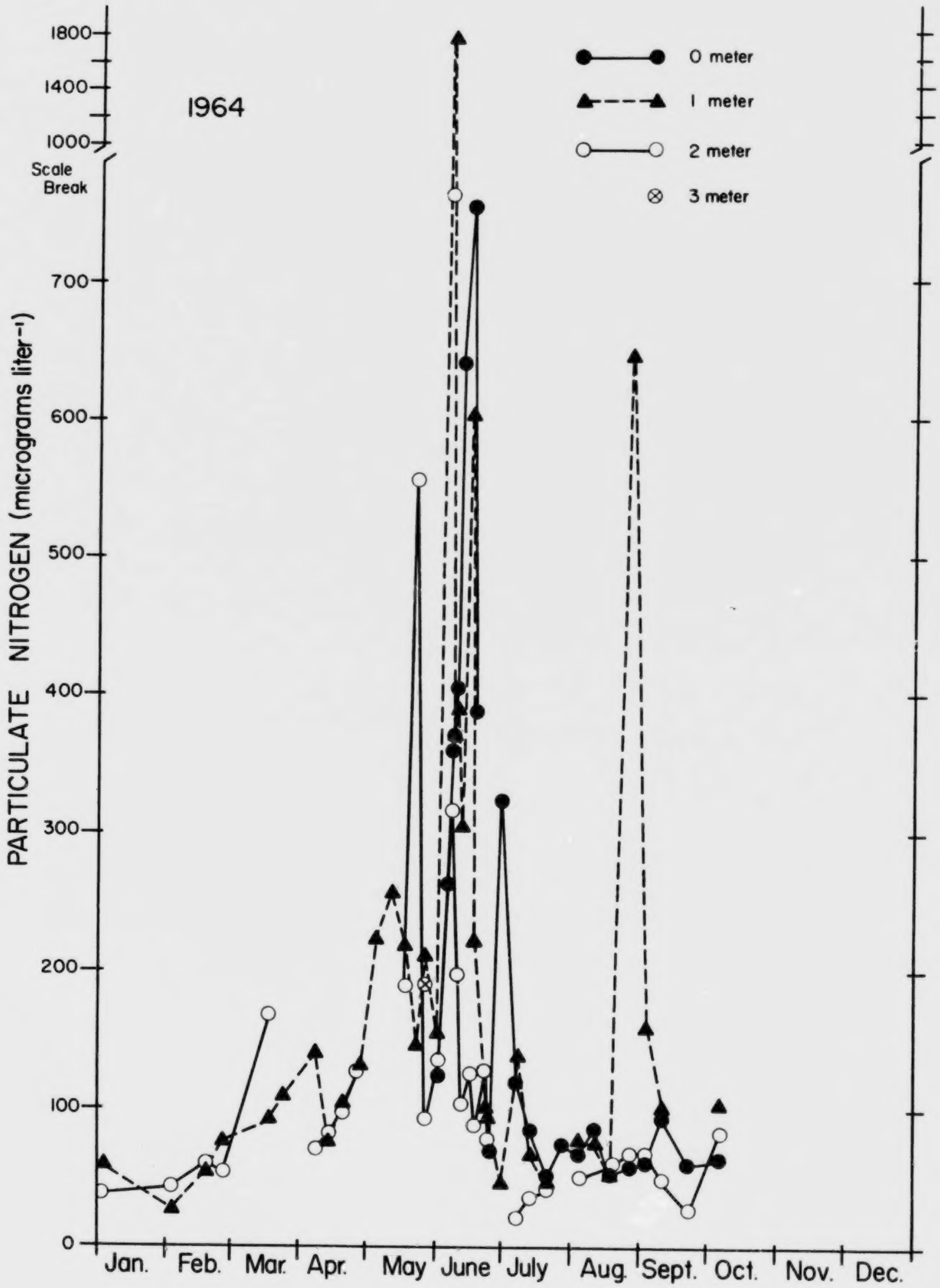

Figure 14. Particulate N, 1964

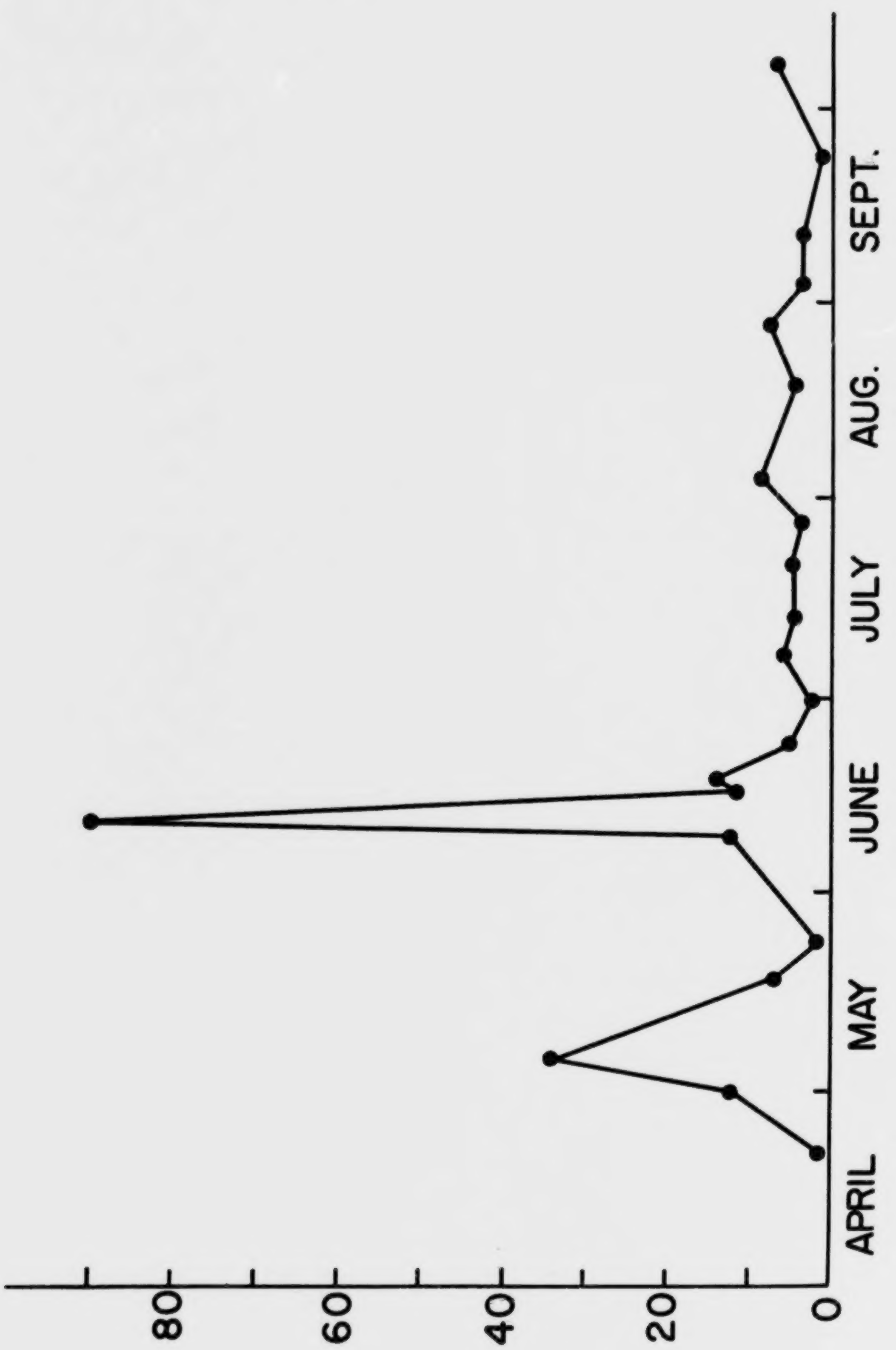

Figure 15. Seasonal primary productivity, 1964.

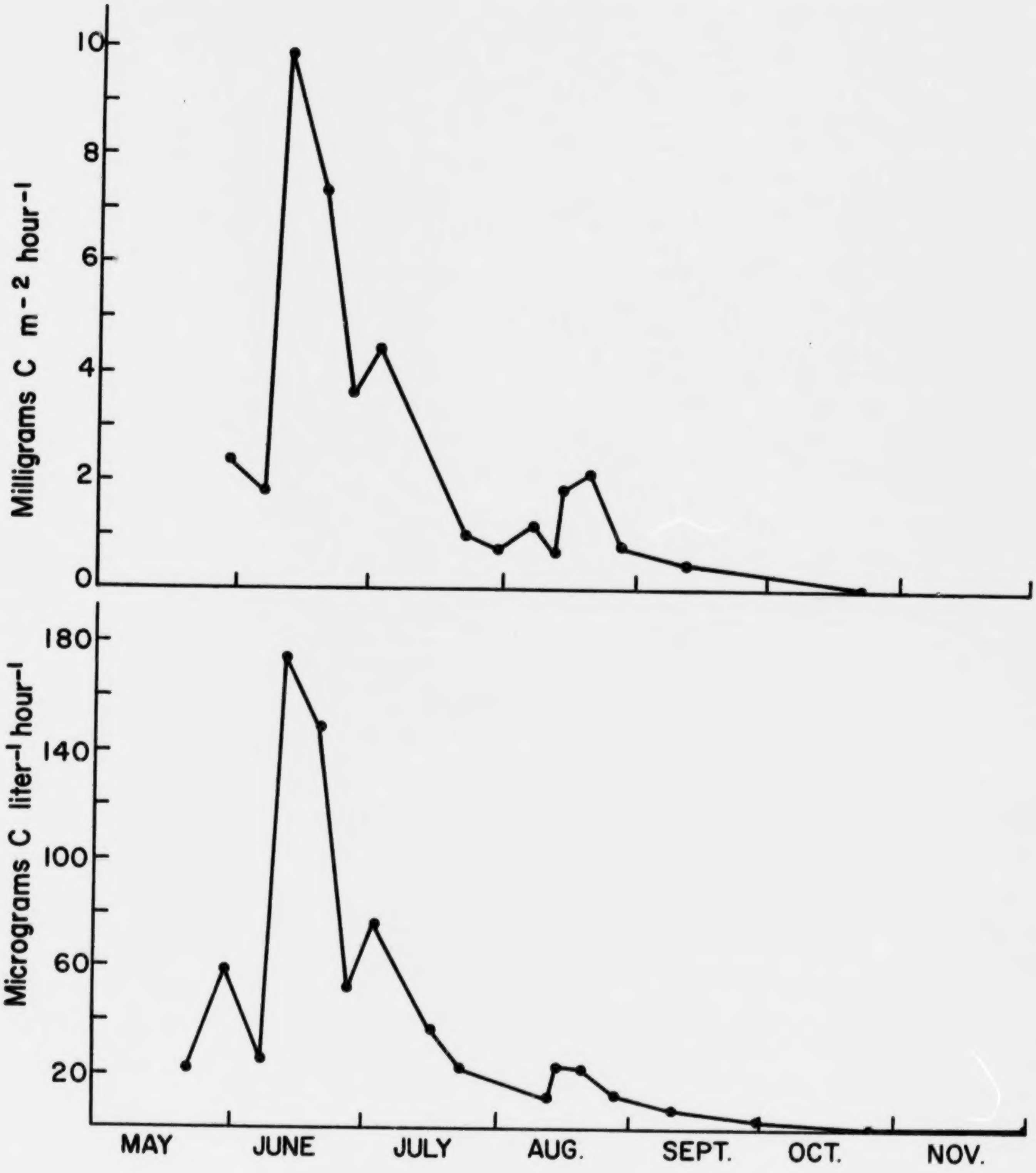

Figure 16. Seasonal primary productivity, 1963.

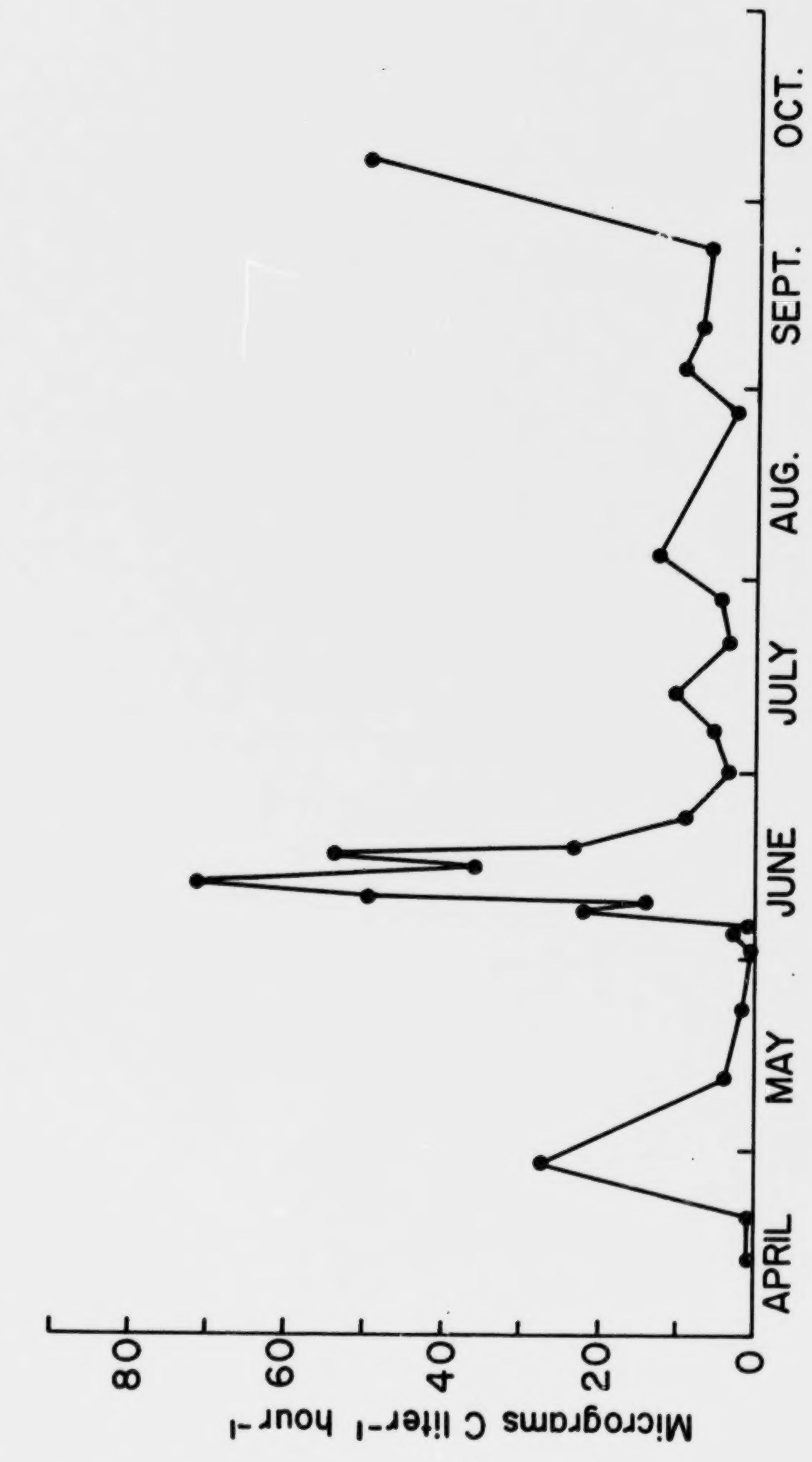

Figure 17. Seasonal primary productivity, 1964 - constant temperature and light.

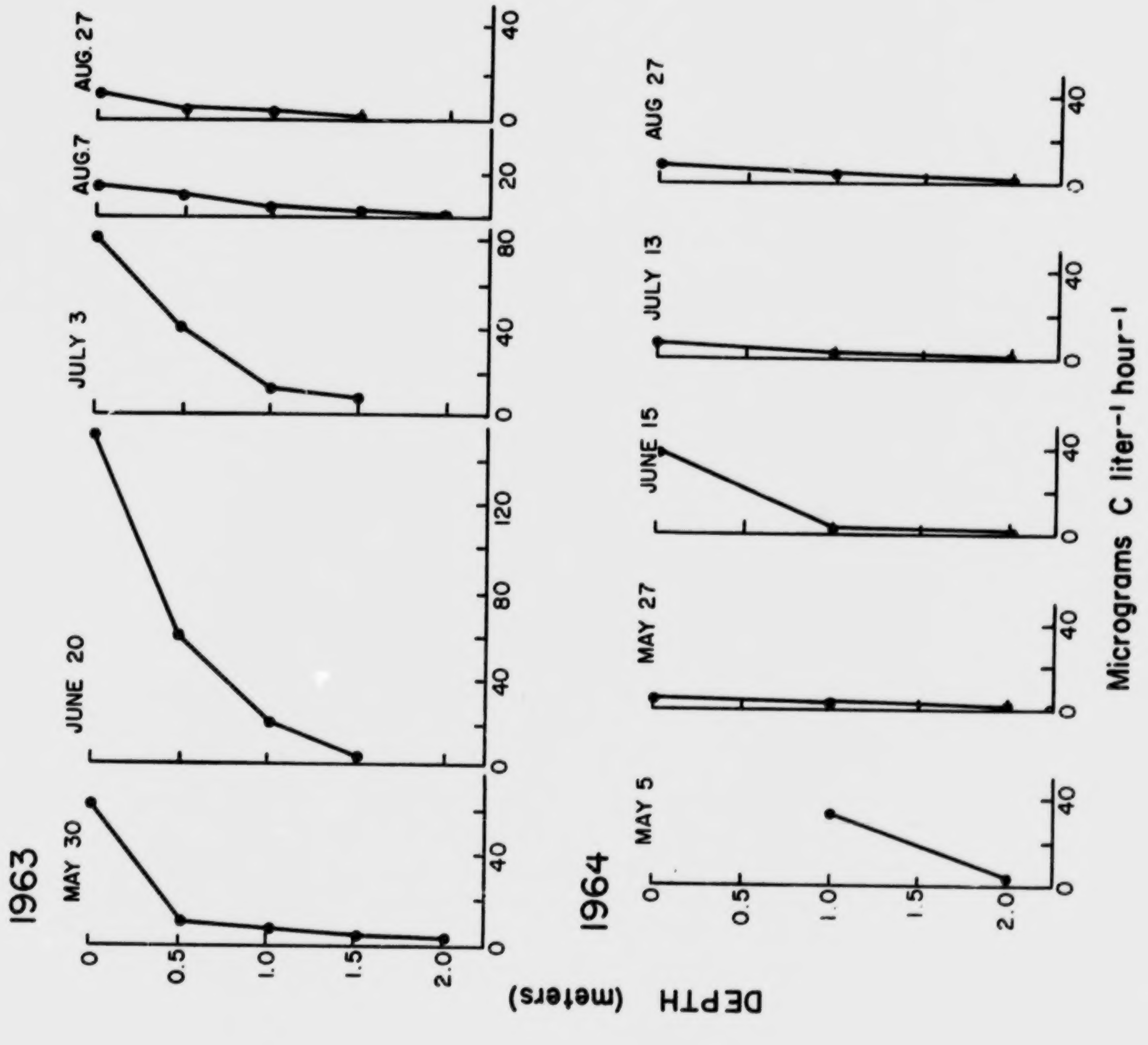

Figure 18. Depth profile - photosynthesis, 1963 and 1964.

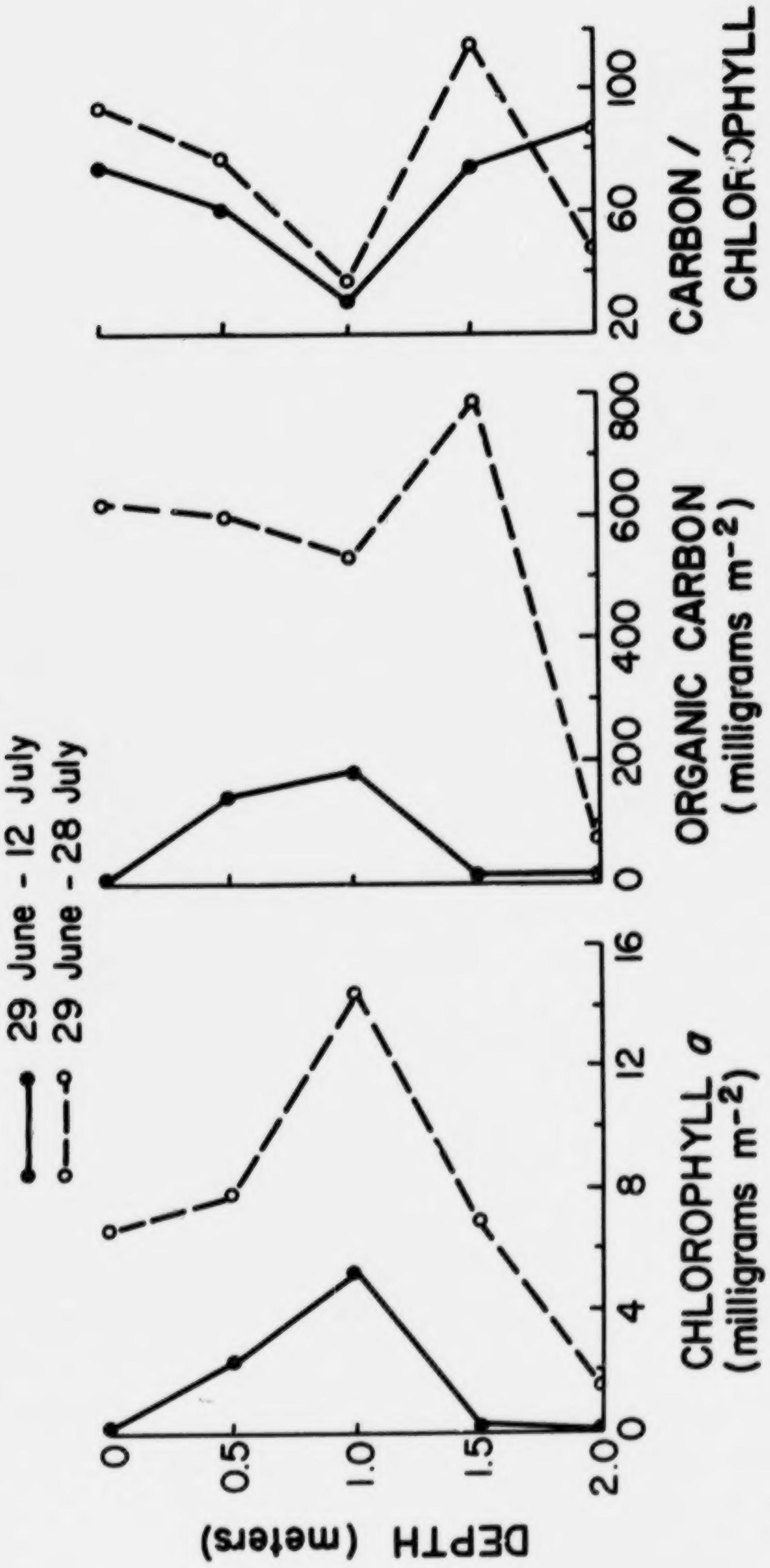

Figure 19. Chlorophyll α and particulate carbon - epiphytes, 1965.

Table 1. Heat budget for Smith Lake water, 1966.

Winter Heat (21 March 1966):

	Depth (m)	Mean Temp. (°C)	Temp. Rise to 4°C (°C)	Volume (m^3)	Heat gain melting (g cal x 10^{-9})	Heat gain water (g cal x 10^{-9})	Total heat gain (g cal x 10^{-9})	Mean heat gain (g cal cm^{-2})
Snow	0.25 to 0.04	(0)	4.0	2,800	223	11	234	164
Overflow	0.04 to 0.00	(0)	4.0	2,800	-	11	11	16
Ice	0.0 to 0.72	0.2	4.0	40,900	3,235	163	3,398	4,854
Water	0.72 to 1.0	0.2	3.8	9,400	-	36	36	51
Water	1.0 to 1.5	0.8	3.2	12,000	-	38	38	54
Water	>1.5	2.4	1.6	11,000	-	27	27	38
								5,177

NOT REPRODUCIBLE

Summer Heat (21 July 1966):

Depth (m)	Mean Temp. (°C)	Temp. Rise above 4°C (°C)	Volume (m^3)	Total heat gain (g cal x 10^{-9})	Mean heat gain (g cal cm^{-2})
0.0 to 0.5	20.9	16.9	31,300	530	735
0.5 to 1.0	19.3	15.3	22,000	336	467
1.0 to 1.5	18.1	14.1	13,000	183	254
>1.5	15.9	11.9	13,500	161	224
					1,680

Annual heat budget: 1,680 + 5,177 = 6,857 g cal cm^{-2}.

Table 2. Extinction coefficients and light penetration in Smith Lake.

Date	k (m^{-1})	Depth of 1% surface light (m)
1 June 1964	2.5	1.8
18 June 1964	2.6	1.8
23 June 1964	3.4	1.4
30 June 1964	3.2	1.5
7 July 1964	3.0	1.5
21 July 1964	2.9	1.5
28 July 1964	2.0	2.3
10 Aug. 1964	2.1	2.2
15 Sept. 1964	2.5	1.8
6 Oct. 1966	3.7	1.3
9 Nov. 1966	3.2	1.0*
Mean	2.8	1.7

*Depth below lower surface of ice which was 0.28m thick.

Table 3. Analyses of the major cations (mg l^{-1}), 1965.

Date	Depth	Ca	Mg	K	Na	Fe	Total Cations (meq l^{-1})
12 July 1965	0m	5.8	7.2	1.6	8.2	0.08	1.29
	1m	5.6	6.0	1.5	6.8	0.18	1.12
	2m	5.6	6.1	1.6	6.6	0.24	1.12
1 August 1965*	Surface	5.2	6.6	1.0	6.0	<0.5	1.09

*Data from Likem and Johnson, 1968.

Table 4. Limnological properties, 1966.

Date	Depth (m)	Temp. (C°)	Dissolved Oxygen (mg l^{-1})	Oxygen Saturation (%)	pH	Total Alkaninity (mg $CaCo_3$ l^{-1})	Dissolved Solids (mg l^{-1})	Conductivity (μmho cm^{-1}, 25°C)	Water Color (Pt units)
25 Feb.	1	0.3	0.0	0.0	6.78	59	169	160	447
	2	2.6	0.0	0.0	6.80	61	170	160	426
25 Mar.	1	0.9	0.0	0.0	6.92	63	172	161	453
	2	2.8	0.0	0.0	6.91	67	171	167	453
21 Apr.	1	0.2	0.0	0.0	6.92	58	175	180	402
	2	2.4	0.0	0.0	6.95	71	181	171	417
11 May	1	1.5	5.5	39	6.75	26	121	87	515
	2	1.6	0.0	0.0	6.84	59	192	169	442
25 May	0	5.3	8.1	64	6.75	24	111	94	375
	1	5.2	6.4	50	6.90	25	112	94	377
	2	5.2	-	-	6.95	27	110	93	-
7 June	0	21.2	-	-	7.76	24	104	89	366
	1	15.3	8.0	79	7.16	26	114	99	384
		9.2	5.7	80	6.79	25	113	98	381
16 June	0	17.6	7.4	77	7.48	28	114	101	334
	1	15.5	6.4	63	7.50	28	111	103	376
	2	7.8	1.2	10	6.74	28	115	103	365
21 July	0	21.3	7.0	78	7.32	29	122	103	326
	1	18.4	7.0	74	7.25	30	120	103	322
	2	16.2	0.6	6	6.85	31	117	107	341
10 Aug.	0	11.7	6.3	58	7.27	30	120	100	299
	1	12.1	7.2	67	7.20	24	118	101	324
	2	11.4	0.8	7	7.28	28	120	103	322
15 Sept.	0	9.5	8.8	75	7.15	29	123	105	308
	1	9.4	8.5	74	7.25	29	125	105	332
	2	9.1	8.6	75	7.15	29	123	105	308
6 Oct.	0	5.5	9.1	72	7.03	27	125	107	296
	2	5.5	9.1	75	7.15	29	128	109	306
9 Nov.	0.3	0.3	8.3	57	6.78	36	148	128	-
	2	3.0	5.2	39	6.85	37	143	128	-

Table 5. Dissolved organic carbon (mg l^{-1}), 1965.

Depth (m)	12 June	30 June	28 July	28 Aug.	6 Oct.	29 Dec.
0	32	-	30	35	32	-
1	32	28	29	26	32	36
2	30	25	-	-	29	34

Table 6. Chemistry of Smith Lake water, 12 May 1966.

	Depth (m)*		
	0.4	1.0	2.0
Temperature (C°)	0.5	3.1	2.2
Dissolved O_2 (mg l^{-1})	9.1	0.0	0.0
pH	6.3	6.6	6.7
Total Alkalinity (mg l^{-1} $CaCO_3$)	8.9	44.4	51.1
Conductivity (μmho cm^{-1}, 25°C)	65	137	166
Total Dissolved Solids (mg l^{-1})	83	158	175
DIP** (μg-at l^{-1})	4.8	1.1	1.1
NO_3^--N (μg-at l^{-1})	1.8	1.0	0.7
$Si(OH)_4$-Si (μg-at l^{-1})	26	31	13

*Depth below top of ice, which was 0.38 m thick.
**Dissolved inorganic phosphous.

Table 7. Nutrients and dissolved oxygen. DIP, DOP and PP refer to dissolved inorganic (reactive phosphorus) dissolved organic (unreactive) phosphorus and particulate phosphous.

Date	Depth (m)	O_2 (mg l^{-1})	NH_4^+-N	NO_3^--N	DIP (μg-at l^{-1})	DOP	PP	$Si(OH_4)$-Si
12 June 1963	0.0	10.5	0.0					
	1.0	8.3						
	2.0	7.5						
19 June 1963	0.0	8.7	2.8					
	1.0	7.5	1.5					
	2.0	5.4	7.7					
26 June 1963	0.0	6.0	0.9	7.8				
	1.0	5.9	1.5	12.7				
	2.0	6.2	3.7	10.8				
7 July 1963	0.0		5.7					
	1.0		9.1					
	2.0		5.7					
20 Aug. 1963	0.0	7.6	3.6					
	1.0	6.8	1.4					
	2.0	6.9	5.7					
27 Aug. 1963	0.0	7.8	3.6					
	1.0	7.7	4.0					
	2.0	7.0	4.7					
3 Sept. 1963	0.0		0.5					
	1.0							
	2.0		0.5					
10 Sept. 1963	0.0		0.5					
	1.0							
	2.0		0.5					
17 Sept. 1963	0.0		3.2					
	1.0							
	2.0							
25 Sept. 1963	0.0	7.2	2.8	1.2				
	1.0	7.8	1.9	1.1	4.6	2.6		
	2.0	8.4	6.0	1.2	4.8	2.8		
9 Oct. 1963	0.0		4.6	3.2	0.3			
	1.0			3.8	0.6			
	2.0			4.0	0.6			
25 Oct. 1963	0.0		6.6		0.5			
	1.0		4.8		0.8			
	2.0		6.3					

Date	Depth (m)	O_2 (mg l^{-1})	NH_4^+-N	NO_3^--N	DIP	DOP	PP	$Si(OH_4)$-Si
					(µg-at l^{-1})			
7 Nov. 1963	0.0		3.2	3.0				
	1.0							
	2.0							
4 Dec. 1963	0.0		ice	ice				
	1.0		8.3	6.4	1.2			
	2.0		11.2	4.9	1.5			
9 Dec. 1963	0.0	ice	ice	ice	ice			
	1.0	6.0		7.7				
	2.0	2.2		5.7				
3 Jan. 1964	0.0	ice	ice	ice	ice			
	1.0	4.0	6.8	9.0	1.9			
	2.0	1.7	23.5	5.3	3.5			
3 Feb. 1964	0.0	ice	ice	ice	ice			
	1.0	0.9	5.3	13.0	2.6	1.9		
	2.0	0.2	6.3	9.0	2.6	2.2		
19 Feb. 1964	0.0	ice	ice	ice	ice			
	1.0	0.1	7.6	10.0	3.2	1.7		
	2.0	0.1	10.2	6.8	3.6	2.3		
26 Feb. 1964	0.0	ice	ice	ice	ice	ice		
	1.0		19.9	4.7				
	2.0	0.1		1.7				
18 Mar. 1964	0.0	ice	ice	ice	ice	ice	ice	ice
	1.0	trace	13.4	1.3	4.2	1.9		
	2.0	0.0	11.4	0.5	5.6	2.4		
24 Mar. 1964	0.0	ice	ice	ice	ice	ice		
	1.0	0.0	29.7	0.3	4.0	1.2		
	2.0	0.0						
8 Apr. 1964	0.0	ice	ice	ice	ice	ice		
	1.0	trace	12.1					
	2.0	0.0	32.7	0.2	4.5	2.0		
14 Apr. 1964	0.0	ice	ice	ice	ice	ice	ice	ice
	1.0		32.1	0.5	3.3	1.1	0.6	10.2
	2.0		46.4		6.0	1.7	0.0	11.7
20 Apr. 1964	0.0	ice	ice	ice	ice	ice	ice	ice
	1.0	0.0		0.3				10.6
	2.0	0.0						
1 May 1964	0.0	ice	ice	ice	ice	ice	ice	ice
	1.0	1.1						8.0
	2.0	trace						

Date	Depth (m)	O_2 (mg l^{-1})	NH_4^+-N	NO_3^--N	DIP	DOP	PP	$Si(OH)_4$-Si
					(μg-at l^{-1})			
5 May 1964	0.0	ice	ice	ice	ice	ice	ice	ice
	1.0	2.3	8.4	3.0	3.5	2.6		11.9
	2.0	0.0			4.1	2.5		
13 May 1964	0.0	ice	ice	ice	ice	ice	ice	ice
	1.0	6.3	7.2	0.0	4.8	1.4		28.2
	2.0	0.5			5.7	2.5		
18 May 1964	0.0	ice	ice	ice	ice	ice	ice	ice
	1.0	8.6		0.2	3.4	1.8		48.7
	2.0	1.7		0.3	4.2	0.9		10.8
23 May 1964	0.0	ice	ice	ice	ice	ice	ice	ice
	1.0	5.3	3.1	0.1	4.4	2.0		17.8
	2.0	0.6	2.7	0.3	3.0	2.4		9.6
27 May 1964	0.0	ice	ice	ice	ice	ice	ice	ice
	1.0	9.6	0.0	0.0	3.4	2.1		
	2.0	9.3		0.5	0.9	10.1		
30 May 1964	0.0		0.4	0.1	3.2	0.7	1.5	28.9
	1.0			0.1	1.7	1.6	0.7	19.4
	2.0			0.5	3.5	2.1	0.7	9.3
8 June 1964	0.0	9.7	0.6		1.6	4.3		
	1.0	8.7			1.5			
	2.0	4.0			2.5			
10 June 1964	0.0	9.8	2.2	0.1	2.0	2.1	14.2	
	1.0	9.6		0.0	2.0	1.0	0.4	
	2.0	3.3		0.5	2.8	1.0	1.6	
12 June 1964	0.0	11.6		0.2	0.3	0.8	2.0	
	1.0	9.4		0.1	1.0	1.5		
	2.0	1.9		0.3	3.0	1.4	0.3	
16 June 1964	0.0	11.5		0.2	0.6	2.4		6.9
	1.0	10.2		0.2	0.3	3.5		9.5
	2.0	1.7		0.6	2.2			4.8
23 June 1964	0.0	6.7		0.3	0.7	0.7	0.1	
	1.0	6.4		0.3	1.0	0.7	0.0	8.5
	2.0	6.2		0.5	2.6	0.6	0.2	
25 June 1964	0.0	6.9	16.5	0.3	0.4	0.8	0.1	1.9
	1.0	6.7		0.4	0.5	0.9	0.0	
	2.0	6.6		0.5	0.4	0.5	0.6	
30 June 1964	0.0	7.9	6.1	1.0	0.3	0.6	0.5	
	1.0	7.9		0.9	0.3	0.6	0.4	
	2.0	4.2		1.7	1.2	0.5	1.2	

Date	Depth (m)	O_2 (mg l^{-1})	NH_4^+-N	NO_3^--N	DIP	DOP	PP	Si$(OH)_4$-
					(µg-at l^{-1})			
7 July 1964	0.0	8.1	6.0	0.5	0.3	0.5	0.4	
	1.0	7.9		0.7	0.2	0.5	2.9	
	2.0	1.4		1.8	2.5		0.3	
13 July 1964	0.0		5.8	0.3				1.9
	1.0			0.5				1.8
	2.0			1.7				1.4
21 July 1964	0.0	7.1	5.1	0.7				1.2
	1.0	6.3		0.8				1.1
	2.0	1.3		1.0				1.2
28 July 1964	0.0	8.0	0.6	0.1				
	1.0	7.8		0.0	0.2			1.3
	2.0	2.9		0.8				1.8
4 Aug. 1964	0.0	7.7	0.2	0.0	0.4			
	1.0	7.7		0.7	0.6			
	2.0	3.9		0.8	1.5			
11 Aug. 1964	0.0	7.9	0.0	0.1				2.1
	1.0	7.8		0.0				1.9
	2.0	4.1		0.6				2.1
18 Aug. 1964	0.0		1.5	0.1				1.8
	1.0			0.1				1.4
	2.0			0.2				2.0
27 Aug. 1964	0.0	8.2	2.7	0.1				2.9
	1.0	8.0						2.3
	2.0	8.0						1.6
3 Sept. 1964	0.0		2.5	0.2				
	1.0			0.2				
	2.0			1.2				
10 Sept. 1964	0.0	9.6	0.1	0.1				2.8
	1.0	9.2		0.2				2.4
	2.0	9.3		0.2				1.4
22 Sept. 1964	0.0	6.9	0.3	0.3				
	1.0	9.0						
	2.0	8.8		0.0				
20 Jan. 1966	0.0	ice	ice	ice	ice			ice
	1.0	3.9	10.6	4.5				
	2.0	0.3		1.0				

Date	Depth (m)	O_2 (mg l^{-1})	NH_4^+-N	NO_3^--N	DIP (μg-at l^{-1})	DOP	PP	$Si(OH)_4$-Si
11 May 1966	0.0	ice	ice	ice	ice			ice
	1.0	5.5		0.9	4.6			38.0
	2.0	0.0		0.4	2.1			24.0
12 May 1966	0.0	ice	ice	ice	ice			ice
	1.0	9.1	21.9	5.5	1.1			31.0
	2.0	0.0		1.0	1.1			13.0
24 May 1966	0.0	ice	ice	ice	ice			ice
	1.0	7.6	8.1	0.3	1.6			0.0
	2.0	7.7	6.5	0.3	1.5			20.0
1 June 1966	0.0	11.1		0.4	0.7			27.0
	1.0	8.6		0.3				
	2.0							
6 June 1966	0.0	8.0	2.6	0.4	0.7			27.0
	1.0	5.7	3.8	0.4	1.0			17.0
	2.0							
14 June 1966	0.0	8.0	7.4	0.0				
	1.0							
	2.0	1.9		0.3				
16 June 1966	0.0	7.4	7.1		0.2			8.0
	1.0	6.4	7.1		0.2			3.0
	2.0	1.2	7.9		1.6			0.0
30 June 1966	0.0	7.8	6.9	0.1				
	1.0	6.0	0.5	0.2				
	2.0	2.0	1.7	0.6				
21 July 1966	0.0	7.0	5.3	0.1	0.2			7.0
	1.0	7.0		0.5	0.2			15.0
	2.0	0.6		0.3	1.3			30.0
10 Aug. 1966	0.0	11.7		0.4				12.0
	1.0	12.1		0.4				10.0
	2.0	11.4		0.2				12.0
19 Aug. 1966	0.0		4.7	0.4				
	1.0							
	2.0							
13 Sept. 1966	0.0			0.1				
	1.0							
	2.0							
15 Sept. 1966	0.0	8.8						
	1.0	8.5						
	2.0	8.6						

Date	Depth	O_2	NH_4^+-N	NO_3^--N	DIP	DOP	PP	$Si(OH)_4^-$
	(m)	(mg l^{-1})			(µg-at l^{-1})			
28 Jan. 1966	0.0	ice	ice	ice	ice			ice
	1.0	1.6		7.9				
	2.0	0.4	5.8	6.3				
3 Feb. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.2	35.7	4.1				
	2.0	0.0		0.5				
15 Feb. 1966	0.0	ice	ice	ice	ice			ice
	1.0		23.8					
	2.0			0.1				
25 Feb. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.0						
	2.0	0.0		0.0				
28 Feb. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.0	53.5	0.2				
	2.0	0.0		0.2				
9 Mar. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.0	35.2	0.1				
	2.0	0.0		0.1				
15 Mar. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.1	40.8	0.1				
	2.0	0.0		0.1				
23 Mar. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.0		0.0				
	2.0	0.0		0.0				
25 Mar. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.0	75.6	0.0				
	2.0	0.0	74.8	0.0				
6 Apr. 1966	0.0	ice	ice	ice	ice			ice
	1.0			0.3				
	2.0			0.1				
9 Apr. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.0	23.8	0.2				
	2.0	0.0	80.4	0.0				
22 Apr. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.0		0.0	1.6			28.0
	2.0	0.0	48.6	0.1	1.8			34.0
28 Apr. 1966	0.0	ice	ice	ice	ice			ice
	1.0	0.0		0.3				
	2.0	0.0	48.0	0.1				

Table 8. Mean concentrations ($\mu g\ l^{-1}$) of transition metals in Smith Lake. Number of samples is given in parentheses.

Period	Depth (m)	Total Cobalt	Total Copper	Dissolved Iron	Total Iron	Particulate Iron (%)	Dissolved Manganese	Total Manganese	Particulate Manganese (%)	Total Zinc
1964 Ice-free	0	-	3.0(11)	98(10)	130(11)	25	4.1(10)	4.7(11)	13	6.2(11)
	1	-	2.6(10)	110(10)	127(10)	13	5.1(10)	6.2(10)	18	8.3(10)
	2	-	4.3(10)	162(10)	176(10)	8	15.8(10)	16.9(10)	7	10.3(10)
1965-1966 Ice-free	0	1.0(4)	2.8(10)	113(10)	139(10)	19	2.5(10)	5.7(10)	56	3.2(9)
	1	0.9(3)	2.5(8)	102(8)	142(8)	28	3.1(8)	6.7(8)	54	4.1(8)
	2	0.9(4)	2.5(10)	114(10)	163(10)	28	5.6(10)	10.7(10)	48	3.5(10)
1965-1966 Ice-covered	1	0.9(1)	1.7(6)	314(6)	372(6)	16	34.2(5)	36.2(6)	5	2.7(6)
	2	0.9(1)	2.0(7)	339(7)	412(6)	18	36.9(6)	37.4(6)	1	2.9(6)
Overall Mean		0.9(13)	2.8(72)	156(71)	188(71)	17	10.8(69)	13.3(71)	19	4.1(70)

Date	Depth (m)	O_2 (mg l^{-1})	NH_4^+-N	NO_3^--N	DIP	DOP	PP	$Si(OH)_4$-Si
					(µg-at l^{-1})			
5 Oct. 1966	0.0	9.1	7.9	0.1				
	1.0		5.6					
	2.0	9.1		0.4				
2 Nov. 1966	0.0		ice	ice	ice	ice		
	1.0		10.3	0.1	0.4	2.4		
	2.0							
9 Nov. 1966	0.0	ice	ice	ice	ice	ice		
	1.0	8.3	6.5	0.4				
	2.0	5.2						

NOT REPRODUCIBLE

Nutrients in the inflow stream:

	NH_4^+-N	NO_3^--N	DIP	DOP	$Si(OH)_4$-Si
5 May 1964	8.04	0.42	5.9	2.6	
18 May 1964	6.58	0.41	1.5	1.5	
27 May 1964	0.23	0.27			
16 June 1964		0.84	0.2	0.7	44
30 June 1964		1.02	0.3	0.7	

Character	Sediment Depth (cm)	Dry Weight (% wet wt)	Water (% wet wt)	Loss from Digestion (%)	Ash* (%)	CO (ppm)	Cu (ppm)	Fe (ppt)	Mn (ppm)	P (ppt)	Zn (ppm)
Aquatic	0.0- 3.3	11	89	41	59	13	50	25	190	1.03	93
Aquatic	3.3- 5.5	21	79	48	52	14	54	27	210	0.87	100
Aquatic	5.5- 8.5	22	78	42	58	15	58	26	210	0.83	92
Aquatic	8.5-11.0	25	75	44	56	16	61	27	210	0.83	94
Mixed	11.0-13.5	29	71	38	62	18	55	30	230	0.83	110
Terrestrial	13.5-16.0	29	71	39	61	19	63	29	240	0.84	140
Terrestrial	16.0-19.0	39	61	45	55	17	81	28	230	0.74	180
Terrestrial	19.0-21.3			58	42	17	96	23	220	0.76	220
Mean of 9 samples from transect across lake:											
Aquatic	0-5	10	90	43	57		55	23	220		99
				Lowest value			48	10	190		79
				Highest value			62	43	260		120

*Perchloric acid insoluble residue

Table 10. ^{14}C primary productivity, 1966. (3 hr laboratory inculations at 25° or 10°C depending on lake water temperature).

NOT REPRODUCIBLE

Date	Depth (m)	Net Productivity (μg C l^{-1} hr^{-1})
1 June	0.0	49.3
	1.0	35.4
7 June	0.0	107.7
	2.0	24.7
10 June	0.0	468.4
	2.5	23.1
14 June	0.0	67.6
	2.2	5.8
16 June	0.0	63.6
	1.0	56.0
	2.5	13.4
30 June	0.0	71.9
	1.0	11.7
	2.5	3.4
10 Aug.	0.0	22.1
	1.0	20.9
19 Aug.	0.0	50.9

NOT REPRODUCIBLE

Table 11. ^{14}C primary productivity, 1967.

Date	Depth (m)	(μg C l^{-1} hr^{-1}) 24 hr *in situ* incubation	Net Productivity (μg C l^{-1} day^{-1}) 24 hr *in situ* incubation	(μg C l^{-1} hr^{-1}) 3 hr laboratory incubation
5 June	0	10.0	240.7	13.6*
	1	2.2	53.2	11.6*
	2	.2	5.5	6.5*
12 June	0			52.1**
	1	3.4	80.7	34.2**
	2	2.0	46.3	7.3**
23 June	0	20.1	483.14	
	1	4.5	108.8	
	2	0.6	15.3	
	3	0	0	
6 July	0	6.4	154.8	10.1**
	1	1.4	34.1	8.1**
	2	4.6	110.2	40.7**

*Incubation at 10°C

**Incubation at 20°C

Table 12. Chlorophyll a concentrations and ^{14}C uptake, and their ratio (*in situ* experiments), 1964.

NOT REPRODUCIBLE

Date	Chlorophyll a (μg l-1)	^{14}C uptake ($\mu g\ C\ l^{-1}\ hr^{-1}$)	^{14}C uptake: chlorophyll a
1 May	10	13.75	1.38
5 May	12	33.5	2.79
18 May	16.4	6.92	.42
23 May	7.1	2.24	.31
27 May	4.5	2.26	.51
1 June	6.8	.84	.12
8 June	22.6	34.10	1.50
10 June	17.1	29.65	1.73
			Anabaena
12 June	132.3	89.74	.68
15 June	62.9	35.68	.57
18 June	29.3	14.91	.51
23 June	5.9	5.29	.90
30 June	7.7	3.34	.43
7 July	3.2	5.76	1.80
13 July	5.7	5.49	.96
			Aphanizomenon
21 July	2.3	4.54	1.96
4 Aug.	4.5	9.06	2.00
18 Aug.	4.0	5.38	1.34
10 Sept.	14	4.34	.31
22 Sept.	10	2.39	.24
6 Oct.	11.7	7.32	.63

Table 13. Winter ^{14}C fixations, 1966. (Incubated for 24 hours in constant temperature room at 5°C under low light).

Date	Depth (m)	^{14}C Fixation (μg C l^{-1} day^{-1}) light	dark
19 Jan.	below ice	0.9	
	1.3	1.1	
3 Feb.	below ice	3.1	2.2
	1.3	38.1	34.7
25 Feb.	below ice		
	1.3	45.1	40.9
28 Feb.	below ice	3.3	2.7
	2	8.6	11.9
9 March	below ice	17.9	16.0
	1.3	15.7	23.5
25 March	below ice	14.5	9.2
	1.3	12.5	9.7
6 April	below ice	29.8	27.5
22 April	below ice	20.8	26.8
	1.3	29.3	29.6
25 May	0	51.7	4.9
	3	569.0	3.5

Table 14. Chemistry and ^{14}C primary productivity of snow, ice and water of Smith Lake, 21 April 1966.

	Thickness (cm)	Water Color (ppm Pt)	$Si(OH)_4$-Si (μg-at l^{-1})	DIP (μg-at l^{-1})	NO_3^--N (μg-at l^{-1})	Chlorophyll a (μg l^{-1})	^{14}C Primary Productivity** (μg C l^{-1} day^{-1})
Snow	26	0	4	0.4	1.5	0.3	2.8
Overflow water	4	43	9	0.4	2.3	6.3	113
Overflow ice	12	6	2	0.7	0.4	0.0	0.0
Overflow ice	19	81	10	0.2	0.7	0.2	0.6
Clear ice	41	0	0	0.1	0.4	0.0	0.0
Lake water	5*	403	28	1.6	0.6	1.3	2.3
Lake water	125*	417	34	1.8	0.7	2.0	0.0

[*] Depth below under surface of ice.

[**] Incubated for 24 hours at 5°C under moderate incandescent illumination (800 lux).

Table 15. Biomass and productivity of benthic plants.

NOT REPRODUCIBLE

Species	Wet wt ($g\ g^{-1}$ dry wt)	Net Oxygen Evolution (mg $O_2\ g^{-1}$ (dry) hr^{-1})	Standing Crop (g dry wt m^{-2}) Depth (m) 0.0-0.5	0.5-1.0	1.0-1.5
Ceratophyllum demersum L.	7.2	5.5	1.5	3.4	0.5
Dreponocladus sp.	7.0	3.8	0.9	1.8	1.6
Potamogeton perfoliatus L.	7.5	2.9	2.0	1.5	0.7
Potamogeton sp.	6.8	6.1	4.5	18.4	0.1
Utricularia vulgaris L.	10.2	2.7	2.3	2.4	0.6
Other			0.8	0.7	2.3
Total			12.0	28.2	5.8
Calculated net carbon fixation (mg C m^{-2} hr^{-1})			21	57	9
Net oxygen production (mg O_2 m^{-2} hr^{-1})			55	153	23

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GEOCHEMISTRY AND PRIMARY PRODUCTIVITY OF THE TANGLE LAKE SYSTEM, AN ALASKAN ALPINE WATERSHED*

Robert J. Barsdate and Vera Alexander

Institute of Marine Science
University of Alaska
College, Alaska 99701

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*Contribution No. XX from the Institute of Marine Science

ABSTRACT

Chemical, biological, and a few physical parameters were determined on six lakes and the major tributaries in the Tangle Lakes.

The waters are of the calcium bicarbonate type and are of low to moderate hardness (16 to 48 mg $CaCO_3$/l). The major ionic components in the lakes decrease downstream in response to more dilute lateral stream inputs. The transition metals cobalt, copper, iron, manganese, and zinc are present at unusually low concentrations, although other nutrients are relatively abundant in the lakes (mean reactive phosphorus 0.4 ug-at/l; nitrate-N 2.7 ug-at/l).

Despite the short (110 day) ice free season and high wind velocities the deeper lakes develop strong thermal stratification, and the lakes surface temperatures reach 17°C late in July. The waters are fairly transparent (extinction coefficients vary from 0.39 to 0.60/m), a factor of importance to the plant productivity of the lakes.

Photosynthetic carbon fixation by plankton algae occurs at modest intensities, the mean in the euphotic zone being *ca.* 80 mg C/m^3-day. However, when integrated over the water column production is as much as 635 mg C/m^2-day which is greater than that of most high latitude lakes.

INTRODUCTION

Few studies have been carried out on lakes in interior subarctic Alaska, and hitherto most of the information on subarctic lakes had derived from work on lakes of the southern coastal regions, especially the Alaska Peninsula (Burgner, 1964; Goldman, 1960) and Kodiak and Afognak Islands (Nelson and Edmondson, 1955; Dugdale and Dugdale, 1961). These studies have invariably demonstrated low lake productivities, and similarly lakes of the Arctic have been shown very unproductive (Kalff, 1967; Hobbie, 1960). However, these results cannot be extrapolated to interior Alaska. This region has a continental climate, and although the low temperature regime in winter equals conditions in the Arctic, the summers are very different from the regimes to the north and to the south.

The Tangle Lakes were selected because earlier work suggested unusually high rates of plankton primary productivity (Dugdale *et al.*, 1961), and because they are relatively free of possible disturbance by man's activity and yet are accessible by road during the important summer season. In addition, the flowing nature of the lakes, with distinct inputs and outputs, makes the system potentially useful for a study of lake processes. This present work is essentially a reconnaissance survey of the limnology of the system.

In addition to the brief work done by Dugdale *et al.* (1961), the U.S. Fish and Wildlife Service in 1953 had initiated studies of the Tangle Lakes in response to the construction of the Denali Highway (completed to the lakes in July of 1954) and the expectation of high fishing intensity of these previously inaccessible waters. Part of this work included a general limnological survey of the lakes (Wojcik, 1954), which has been especially useful in planning the investigation reported here. Since then the Alaska Department of Fish and Game has been working on the Tangle Lakes with reference to sport fisheries management (*cf.* Heckart, 1965; Shallock, 1966).

METHODS

Most of the lakes were sampled from a light, flat-bottom boat, but Second and Lower Tangle Lakes were reached by float-equipped light aircraft. Winter observations were made also from small aircraft, in this case on skis.

The map (Figure 1) was redrawn from U.S. Geological Survey 1:63,360 Series topographic maps, Mt. Hayes and Gulkana Quadrangles. Watershed areas and lake surface areas were determined by planimetry of enlarged copies of the USGS maps.

Temperature and light were measured in the lakes with a Whitney combination probe at depth intervals of 1 m or less. Extinction coefficients (k, as defined by Strickland, 1958) for light were determined graphically from semilogarithmic plots of light intensity vs. depth. Stream discharge was measured with wood floats employing Embody's formula (Welch, 1948) with correction for bottom roughness.

Water samples were collected with an opaque, nonmetallic water sampler and protected from direct sunlight during transport to the field laboratory. Measurements of pH and alkalinity, and filtration of samples for water color, chlorophyll, particulate matter, major cations, nutrients, and trace metals were performed within 2 to 4 hours after sample acquisition. Samples for major cations (calcium, magnesium, potassium, and sodium), for trace metals (cobalt, copper, iron, manganese, and zinc), nutrients (ammonia, nitrate, nitrite, silicate, and soluble phosphorus), and chlorophyll were filtered through glass fiber filters (Reeve Angel 984-H Ultra). The filters were frozen for pigment determinations and the filtrate frozen for nutrient analyses.

Total alkalinity, pH and chloride (specific ion electrode) were determined with a Coleman 37A pH meter, and conductivity with a General Radio Company 1650-A impedence bridge on samples thermostated to 25°C. Dissolved oxygen, total dissolved solids, and particulate matter were determined following techniques of the American Public Health Association (1960), using the azide modification of the Winkler oxygen method, drying 100 ml filtered water samples at 105°C for dissolved solids, and filtration through prewashed, tared 0.45 μm membrane filters for particulate matter. To compensate for the altitudes of the lakes, the oxygen saturation values were calculated assuming a barometric pressure of 684 mm Hg. Sulfate was reduced to sulfide by the method of Luke (1949), trapped in dilute sodium hydroxide and determined as sulfide using the standard methylene blue technique (American Public Health Association, 1960).

Measurements for water color were made at 380 nm with a Beckman DU spectrophotometer and converted somewhat arbitrarily to cobalt-platinum units (mg Pt/l) by multiplying the absorbance by a factor of 3000/cell length in cm. This value was obtained from Zimmerman's (1962) data on water color. The numerical values obtained in this manner are not directly equivalent to those obtained by comparison with cobalt-platinum standards and probably overestimate the conventional water color determination (cf. American Public Health Association, 1960) by 20 to 40 percent.

Major cation analyses were made with a Perkin-Elmer 303 atomic absorption spectrophotometer. Strontium was added to avoid anion interferences in the determinations of calcium and magnesium (Angino and Billings, 1967); sodium was added to samples and standards for the potassium determinations to buffer a slight ionization interference.

Samples for the analysis of cobalt, copper, iron, manganese, and zinc were concentrated by boiling, wet ashed with perchloric acid, and diluted to 1.00% of their original volume. The determinations were made by atomic absorption spectrometry employing corrections for yield, blanks, and interferences. A few iron samples were determined without preconcentration.

Ammonia was determined by the oxidation method of Richards and Kletsch (1964). Reactive phosphorus (RP), nitrate, and nitrite concentrations were measured according to Strickland (1965), the latter two methods being slightly modified in that internal standards were employed. Total dissolved phosphorus (TDP) and total phosphorus (TP) were determined by perchloric acid digestion of filtered and unfiltered water samples, followed by sodium carbonate neutralization and phosphorus determinations as above. Soluble unreactive phosphorus was calculated as the differences between TDP and RP, and particulate phosphorus as the differences between TP and TDP. Reactive silica was determined as *a* silicomolybdic acid (Grasshoff, 1964) on a Technicon Autoanalyzer.

For the determination of chlorophyll *a*, glass fiber filters and their associated particulates were macerated in 90 percent acetone and extracted in the dark at 3°C for 24 hours. After centrifugation the absorbance of the extracts was measured at 658 nm and chlorophyll *a* estimated according to Dugdale (1965).

Photosynthetic carbon fixation was measured by the ^{14}C method (Steemann Nielsen, 1952). Light and dark bottles were incubated *in situ* for 24 hours, filtered (Millipore HA membrane filters, 0.45 μm pore size), rinsed with 5 ml of dilute (0.005 N) HCL, and dried for subsequent radioactivity assay. While the productivity rates observed in these measurements could have little effect on $pC0_2$, pH, and 0_2 during a 24-hour incubation, restriction of circulation and other bottle effects may influence the activity of the confined organisms. It is probable that these 24-hour incubations somewhat underestimate primary productivity rates.

DESCRIPTION OF THE STUDY AREA

The Tangle Lakes watershed, about 300 km northeast of Anchorage, Alaska, contains about a dozen small lake basins interconnected by the Tangle River (see Figure 1). Although at an altitude of less than 900 m, the area is tundra with grasses, alder, willow, sedge, moss, and lichen predominating. The high latitude (63°N) and perhaps also the influence of adjacent high mountains mediate the transition from taiga to tundra at such a low elevation.

The bedrock in the Tangle Lake area consists predominantly of basic extrusive volcanics of Triassic age. The area has been repeatedly glaciated, and the last major glacial advance (in late Quaternary time, *ca* 11,000 years B.P.) covered the area with a rather shallow ice sheet through which the larger hills projected. This ice sheet stagnated and melted, leaving an uneven ground moraine covered with eskers and other ice contact features (Péwé, 1965). The lakes lie in this coarse, unconsolidated glacial material; in the lake basins and channels bare rock ranging upward in size from coarse gravel is predominant. Near the inlet streams are areas of heavy siltation, and the basins of the uppermost lakes (First and Second Tangle Lakes) are flat and shallow, having received much fine sediment.

First Tangle Lake lies at an elevation of 880 m and Lower Tangle Lake 30 km to the north, at 840 m. About half of the total loss of elevation occurs between Long Tangle and Round Tangle Lakes over a distance of about 2 km. Below Round Tangle Lake, the Tangle River is marginally navigable by riverboat, the principal hazard being rocky, shallow water rather than high stream velocities.

A number of lakes in this area occupy rather restricted watersheds and have neither outlets nor well defined inlets. The small excess of precipitation over evaporation in these lakes presumably is discharged into the highly permeable glacial sediments which surround the lakes. The largest of these landlocked lakes, Upper Tangle Lake, was sampled in the present study along with the lakes drained by the Tangle River.

From the northwest to the southwest the surrounding area is drained by the Maclaren River into the Susitna River, which flows west and south into Cook Inlet. The area from the southwest to the east is drained by the Middle Fork of the Gulkana River going south through the Copper River into the Gulf of Alaska. The Tangle River watershed, although located on the south flank of the Alaska Range, flows north into the Delta River and through the Range into the Tanana River, which empties into the Yukon River and on into the Bering Sea.

CLIMATE

The number of hours of sunlight received by the region in which the Tangle Lakes are located varies from more than 20 hours per day in June to about 5 hours per day in December. The lakes are bound on the south by low hills which provide considerable shading from direct sunlight as a result of the low solar elevation at this latitude.

In 1960 a weather station was established at Paxson, 27 kilometers east of the Tangle Lakes. Unfortunately, the weather observations there have been incomplete and discontinuous, and the resultant means (Table 1) are therefore somewhat suspect. Johnson and Hartman (1969) plotted a general precipitation map for Alaska based on the data of Watson (1959). On this map the Tangle Lakes area is in a zone of 16 inches (41 cm) mean annual precipitation. Again, the estimate is rather uncertain, as the weather stations used are rather far removed from the Tangle Lakes area.

HYDROLOGY AND MORPHOLOGY

Wojcik (1954) commented on the large flow rate through the lakes, noting their resemblance to pools in a stream. On 12 July 1953 he measured the flow rate of the Tangle River into Round Tangle Lake as about 5 m^3/sec. This point is downstream from approximately 60% of the drainage area of the entire system. On 31 July 1967 the flow rate at the same point was estimated to be 15 m^3/sec. The flow rates for the tributary streams as recorded in Table 2 were taken during a period of wet weather; and persistent moderate to heavy rains had covered the area for a period of two days before the measurements were made. The Tangle River and Landmark Creek, having comparatively large lakes in their watersheds, were rising slowly in response to the precipitation. Rock Creek and Clear Creek had perhaps tripled their flow rates in the 24 hours prior to measurement.

Because of the large flow volume through the Tangle River system and the small size of the lake basins (Table 3), the residence time for water in these lakes is short. With the possible exception of the south basin of Tangle Lake, a volume of water equal to that of each lake enters each basin in an interval of much less than one year. In the case of Round Tangle Lake the residence time for water would be 30 days at a flow rate of 5 m^3/sec.

THERMAL CHARACTER

Ice cover forms on the lakes and streams by mid-October, although some open water can be found in and near the streams during the winter. Since the road to the lakes is impassable from November through June, only a few rather limited observations have been made during the winter months. In 1968 the lakes were visited on April 10, probably a time close to the period of maximum ice thickness. The snow cover was quite thick, *ca.* 0.5 m on the central portions of the lakes. First Tangle Lake was frozen to the bottom and the ice thickness was 1.3 m, which is rather remarkable in that the maximum observed water depth is 1.0 m. Periodic overflows, presumably from the Tangle River, had intruded the snow cover over the lake ice and had frozen in place, thereby increasing the ice thickness. Second Tangle Lake was frozen to a depth of 0.85 m, and the ice thickness increased slightly downstream through the system to 0.95 m, on Lower Tangle Lake.

The time of spring breakup is variable, with Wojcik (1954) reporting June 13, 1953 and June 8, 1954. Warner (1955) mentioned that the lakes had just undergone breakup and still were circulating freely on the weekend of July 4, 1955. E. W. Shallock noted ice on Round Tangle until June 29, 1965 and estimates June 20 as the mean date of breakup (pers. comm., 1965).

Since breakup occurs near the time of the summer solstice, heat transfer to the water is very rapid, and thermal stratification appears less than ten days after the ice leaves the lakes. The highest recorded surface water temperature was 62°F (17°C) on 25 July 1953 (Wojcik, 1954). The time lag between maximum solar input and maximum water temperature, *ca.* 31 days, is somewhat longer than the corresponding seasonal lag (18 days) to maximum mean air temperature (Johnson and Hartman, 1969). The July 30 to 31, 1967 surface water temperatures (see Figure 2) are probably a few degrees lower than usual, as the preceeding week had been windy, wet, and unseasonably cold. The 1966 thermal data indicate that the fall mixing is almost complete early in September.

CHEMISTRY

Of the ionic components of Tangle Lake waters (Table 4) calcium and bicarbonate are the most abundant. The major cations in order of decreasing weight concentrations are calcium, sodium, magnesium and potassium; however, on the basis of equivalents per liter magnesium is more abundant than sodium. The ratios of the cations are rather constant in the waters sampled, although a slight increase in calcium and a decrease in magnesium is present down stream from Rock Creek. In terms of percent of total equivalents of cations, calcium varies from 57 to 70, magnesium from 15 to 26, sodium from 13 to 16 and potassium from 1.2 to 1.9. Of the anions chloride and sulfate are an order of magnitude less abundant than bicarbonate. The pH of these samples was under 7.8 and consequently carbonate is unimportant. However, pH values up to 9.8 have been observed (Table 5) and carbonate would be relatively abundant under these conditions.

The summer pH of the surface waters usually is between 7.5 and 8.5, with the exception of the shallow terminal lakes (First and Second Tangle) where the pH exceeds 9.5. The bottom waters of the deeper lakes have a somewhat lower pH. Variation in pH found in these lakes seems directly related to the CO_2 cycle, with high pH being caused by photosynthetic uptake of inorganic carbon and lower pH resulting from the release of CO_2 during the oxidation of organic matter in the hypolimnetic waters.

On 17 June 1963 Round Tangle was nearly isothermal (4.2 to 4.5°C) and uniform in dissolved oxygen concentration (9.8 - 10.2 mg/l, *ca.* 85% of surface saturation) to a depth of 27 m. The other lakes, while not sampled, presumably also were uniformly high in dissolved oxygen during this period of vernal circulation. By the end of July the surface waters remained near saturation but a substantial hypolimnetic oxygen deficit developed, and the deeper parts of Tangle and Round Tangle were *ca.* 50% saturated. Wojcik (1954) reported that oxygen concentrations decline to 4.0 mg/l in the deepest waters of Round Tangle and 2.5 mg/l in Shallow Tangle on 12 August. On 4 September 1966 the lakes were actively circulating and consequently well oxygenated with the exception of the deepest waters of Tangle Lake, where the dissolved oxygen concentration at a depth of 18 m had decreased to 2.0 mg/l or 18% of surface saturation.

Conductivity, alkalinity, and dissolved solids all tend to be rather low in these waters and the range of concentration of total dissolved substances is 31 to 78 mg/l. The concentration of dissolved components tends to decrease down river through the system, as the waters of the two largest lateral streams (Rock Creek and Landmark Creek) contain the least dissolved substances in the system. Solids and alkalinity increase in a linear manner with conductivity (Figure 3). A curve fitted to the dissolved solids data would indicate *ca.* 10 mg/l at zero conductivity. In large part this is due to dissolved silica, which is abundant in the system; however, dissolved organics and possibly other poorly ionized solutes and colloids also are present. A Second Tangle Lake sample taken in August shows the greatest deviation from the solids curve, and since the water color of this sample is also high, it is probable that dissolved organic substances are relatively more abundant in this lake than in the downstream parts of this system where the water is not highly colored.

Aquatic macrophytes may excrete a significant portion of photosynthetically fixed carbon (Wetzel, 1969) and it seems likely that the water color here is largely a result of excretion by the vascular aquatic plants which are particularly abundant in First and Second Tangle Lakes. A water sample was taken from Second Tangle in April when the photosynthetic activity of the vascular aquatics was very low, and the water color of this sample was much less (41 Pt units) than in a sample taken in August (119 Pt units). The inorganic ions as represented by conductivity and alkalinity were similar to the previous summer values; however, the dissolved solids were 13 mg/l less than the summer values, a difference perhaps representing the decrease in dissolved organic material from summer to winter conditions.

The 25 m water in Round Tangle is somewhat more dilute than that found overlying it. It is conceivable but not likely that this is a remnant of the water present in the basin prior to the establishment of thermal stratification. Considering the unconsolidated and highly permeable nature of the surrounding terrain, it is not unlikely that this somewhat anomalous water is a result of a subaqueous discharge of ground water directly into the lake basin. The small but sustained flow maintained through the winter at least in the upper reaches of the system is another circumstance suggesting the entry of ground water into the Tangle Lakes system.

Particulate material in Upper Tangle, which has neither inlet nor outlet streams, was extremely low (0.1 mg/l) and in the other lakes and streams ranged from 1 to 6 mg/l.

The trace metal concentrations in the Tangle Lakes (Table 6) are well below the average for Alaskan lakes (Barsdate 1967; Kalff 1968). As with the total dissolved solids, the trace metal concentrations tend to decrease downstream in the system, although there are exceptions and the pattern is not strongly developed. Second Tangle Lake is somewhat unusual in its high concentrations of dissolved iron (160 μg/l), which in well-aerated surface water suggests organic ferrous iron complexes and/or colloidal iron stabilized by organic material. High iron and manganese concentrations also occur in the deeper parts of the hypolimnion of Tangle and Round Tangle Lakes.

The dissolved silica levels (Table 7) are high in the lakes (78 μg-at/l) and extremely high (113 μg-at/l) in the streams. There is no reason to suppose that silica depletion ever limits diatom production in these lakes, but these concentrations may be toxic to some algae (*cf.* Chu, 1942).

Surface waters from lakes of the Tanana Valley, north of the Tangle area, typically contain 0.2 μg-at/l reactive phosphorus and 0.3 μg-at/l nitrate-N (Dugdale, 1965; Barsdate, 1967), while Lake Louise, which is 80 km south of the Tangles has undetectable amounts of reactive phosphorus (<0.02 μg-at/l) and 0.3 μg-at/l nitrate-N (Barsdate, 1967). The reactive phosphorus levels in the Tangle Lakes (0.4 μg-at/l) are about twice those of the Tanana Valley Lakes, and the nitrate-N values (2.7 μg-at/l) are much higher than those of the Tanana Valley lakes or Lake Louise.

The headwaters of the Tangle River through Second Tangle and into Upper Tangle contain the highest concentrations of phosphate and combined nitrogen in the system (Table 7). Rock Creek also has comparatively high nitrogen concentrations but less phosphate. The other major inlet stream, Landmark Creek, has the lowest nitrate and phosphate levels. Particulate and unreactive dissolved phosphorus levels covary with the inorganic nutrients, suggesting that increased levels of these phosphorus fractions result as a biological response to high reactive phosphorus concentration. Nitrate is undetectable in most of the streams and is present in low concentrations in the lakes. Although the levels are very low, nitrite maxima occur at the thermoclines in Long Tangle and Round Tangle Lakes, suggesting that recycling of combined nitrogen is occurring in the waters of those lakes. These two lakes, in which the depth of water greatly exceeds that of the euphotic zone, exhibit somewhat higher nitrogen and phosphorus levels in the deeper waters. The decrease in phosphorus and, to a lesser degree nitrogen, down through the lake system is to some extent the result of dilution by the nutrient-poor lateral stream. In addition, particularly in the instance of the low values in Round Tangle, *in situ* biological utilization and removal from the water column seems likely (see the productivity discussion below).

BIOTA AND PRODUCTIVITY

Previous biological observations in the Tangle Lakes by Wojcik (1954) have indicated substantial fish populations, including Arctic grayling, lake trout, round Whitefish, burbot and sculpin. The same author has described the bottom invertebrates as consisting of annelid worms, nematodes, *Chironomus* sp., *Gammarus* sp., pea clams and snails. Plankton appeared abundant in the lakes, with up to 1 cc per 1000 cc recovered using a no. 12 (125 meshes/inch) net. *Diaptomus* was the dominant component. Aquatic vegetation included extensive areas of *Potamogeton*, *Myriophyllum*, and some *Eleocharis* and *Ranunculus*.

During the present study heavy growths of filimentous algae were observed in shallow water on the lake bottoms and loosely attached to *Potomageton*. On August 1, 1967, much of this material was floating to the surface in mats and strands and was moving down river. In addition benthic diatoms grew in abundance on rocky substrates in the river channels connecting the lake basins. The importance of these benthic components to the overall productivity of the system, and their interaction with dissolved nutrients is presently unassessed.

Quantitative estimates of planktonic algal populations have not been made in these lakes and the present study has used chlorophyll levels and primary production determinations as the major biological parameters. A single ^{14}C primary productivity measurement in August, 1960 had suggested rather high photosynthetic rates in Round Tangle Lake, since a rate of 900 mg C/m^3-day was measured (Dugdale *et al.*, 1961). However, no comparably high rates were observed during the present study.

On a unit volume basis, the photosynthetic rates in the Tangle Lakes were rather modest (Table 8) with a daily mean of 82 mg C/m^3 in the euphotic zone. However, the clarity of the water resulted in a relatively higher total production on a unit surface area basis (361 mg C/m^2-day). The depth of the euphotic zone, as estimated by the depth of penetration of 1% of the surface incident light, compared with other Alaskan lakes was great, in every lake exceeding 5 m, and in some of the lakes it was greater than 10 m. Surface inhibition was a common feature in the lakes, with the photosynthetic maximum usually occurring somewhat below the surface (Figure 4).

The overall trend in the lake system appears to be a decrease in primary productivity downstream, which may be related to the nutrient distribution in the lakes.

The higher rates of photosynthesis and the higher chlorophyll content of the waters during September relative to the July values suggest the occurrence of a fall pulse (Table 8). The possibility of a spring bloom has not been investigated, although such blooms have been found important in other subarctic lakes (Dugdale, 1965). Thus, the results presented here cannot be readily extrapolated to provide annual estimates. However, the productivity of the Tangle Lakes appears to be reasonably high for unpolluted lakes at this latitude, being somewhat higher than those described by Likens and Johnson (1968) for the lower altitudes of interior Alaska. These authors give an estimated productivity for Pullin Lake of about 200 mg C/m^2-day which approaches the levels found in the Tangle Lakes. Other lakes of this latitude, but at altitudes similar to the Tangles and in alpine tundra, have shown considerably lower productivity rates (Dugdale *et al.*, 1961).

DISCUSSION

The importance of fluvial processes in this watershed no doubt have been underemphasized here. The Tangle River is a prominent feature of the system, and the circulating waters of the lakes can be regarded as rather small reaction and settling chambers in a flowing system. Only in the hypolimnions of the lakes, where oxygen is depleted and some of the more labile minor constituents are enriched, is there much difference between lake and river water.

The chemical properties of the Tangle Lakes vary in response to the composition of the inlet stream waters. Tangle Lake water with dissolved solids of ∿70 mg/l mixes with about an equal volume of Rock Creek water (d.s. ∿30 mg/l) to produce water of ∿50 mg/l dissolved solids in the north basin of Tangle and in Round Tangle. The net effect of the contributions of Clear and Landmark Creeks is to further dilute the water, and the downstream lakes - Shallow, Twin, Long and Lower - have ∿40 mg/l dissolved solids.

The proximate source of phosphate is in the upper reaches of the Tangle Lakes, Second Tangle having *ca.* twice the mean concentrations of the lake system. The decrease through the system in part can be attributed to the low levels of nutrients in the lateral streams, but utilization by the plant populations is perhaps the dominant mechanism. The high productivity rates of plankton algae and the well developed benthic plant communities indicate that conditions are less limiting here than in many other high latitude lakes. The favorable nutrient conditions and the relatively high transparency of the water are important factors in photosynthetic activity, and for plankton algae the Tangles are among the more productive high latitude lakes, although they are oligotrophic according to the standards of temperate climates. The maximum productivity which might be anticipated by extrapolating our results would be about 10 g C/m^2/month during a period of three months (June, July and August). This would amount to about 30 g C/m^2/year, which is typical of an oligotrophic lake in temperate regions (Steemann Nielsen, 1959). However, compared with the production of Imkpuk Lake (Kalff, 1967), Lake Schrader (Hobbie, 1960) or Bare Lake (Nelson and Edmondson, 1955), our lake is considerably more productive. In respect to this relatively high productivity the extremely low levels of transition metals are notable and suggests that these elements may not be required in abundance.

ACKNOWLEDGMENTS

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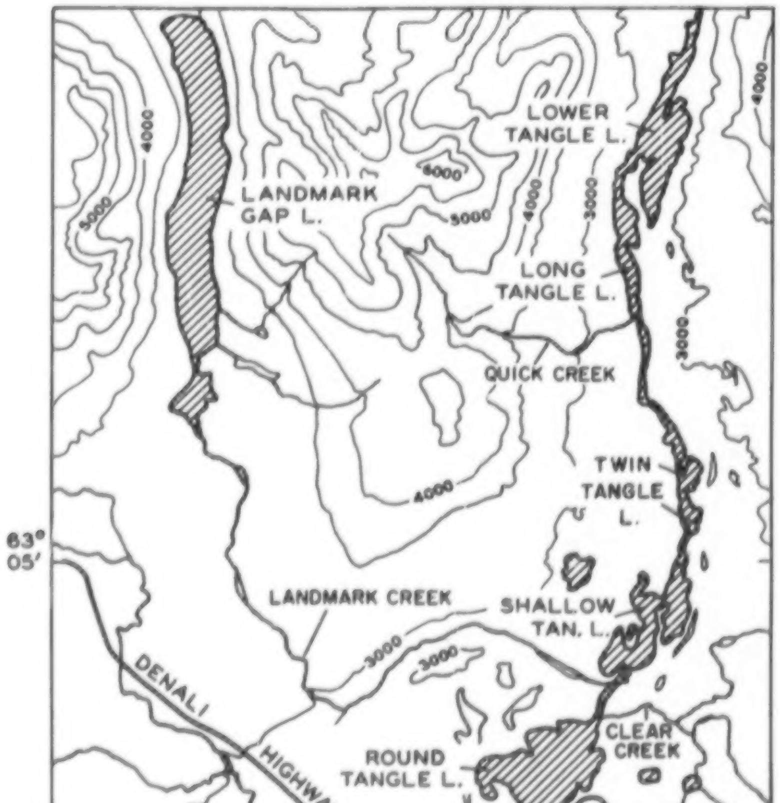
LANDMARK GAP L.
LOWER TANGLE L.
LONG TANGLE L.
QUICK CREEK
TWIN TANGLE L.
LANDMARK CREEK
SHALLOW TAN. L.
DENALI HIGHWAY
ROUND TANGLE L.
CLEAR CREEK
ROCK CREEK
TANGLE L.
UPPER TANGLE L. (LAND-LOCKED)
SECOND TANGLE L.
LITTLE LANDLOCKED TAN. L.
FIRST TAN. L.
ALASKA
STUDY AREA
TANGLE LAKES
0 1 2 Mi.
0 1 2 3 KM.
N. MAG. N. 29.5° E.
63° 05'
63°
146°05'
146°
3000
4000
5000
6000

Fig. 1. Map of the study area (elevations in feet).

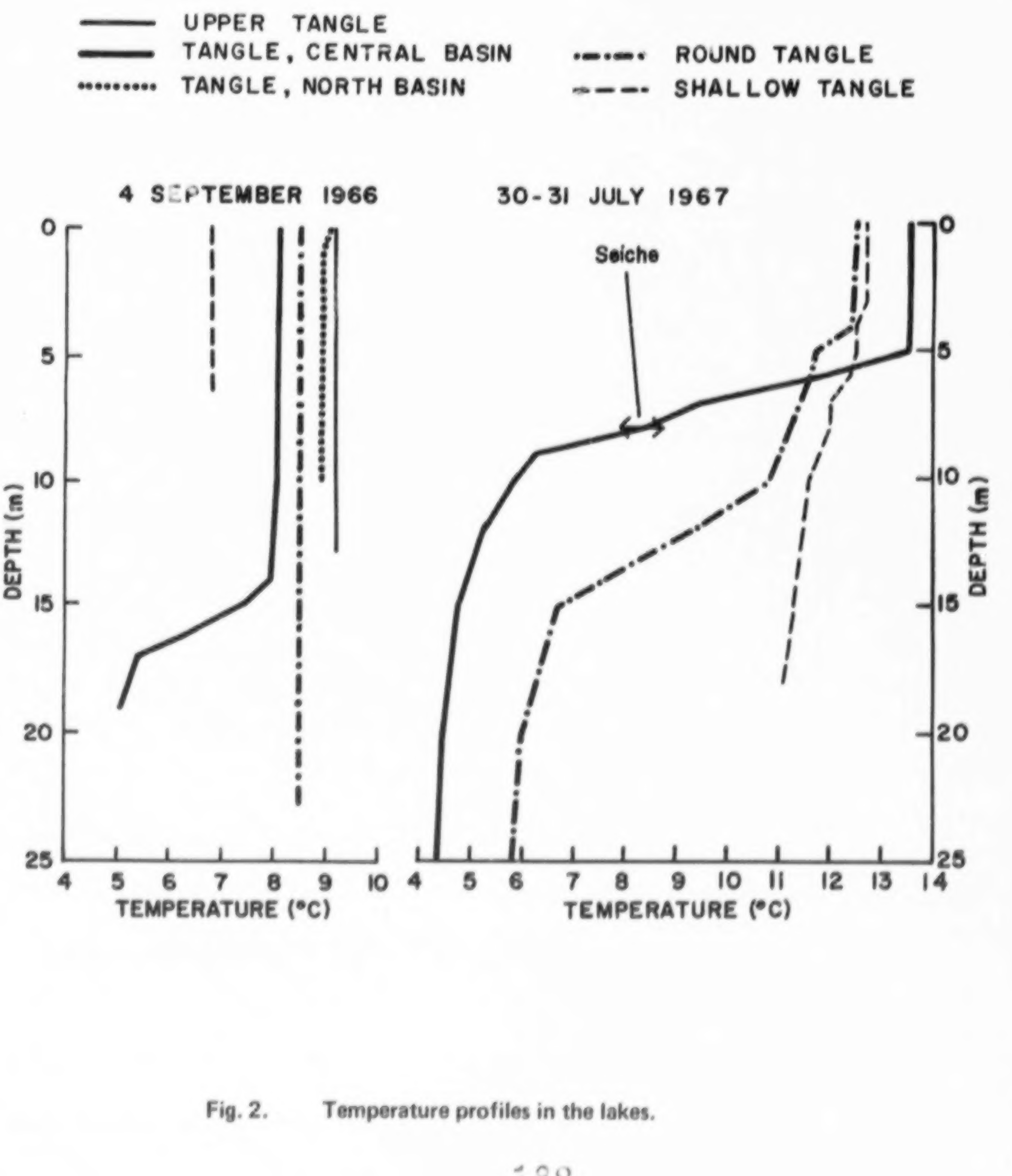

Fig. 2. Temperature profiles in the lakes.

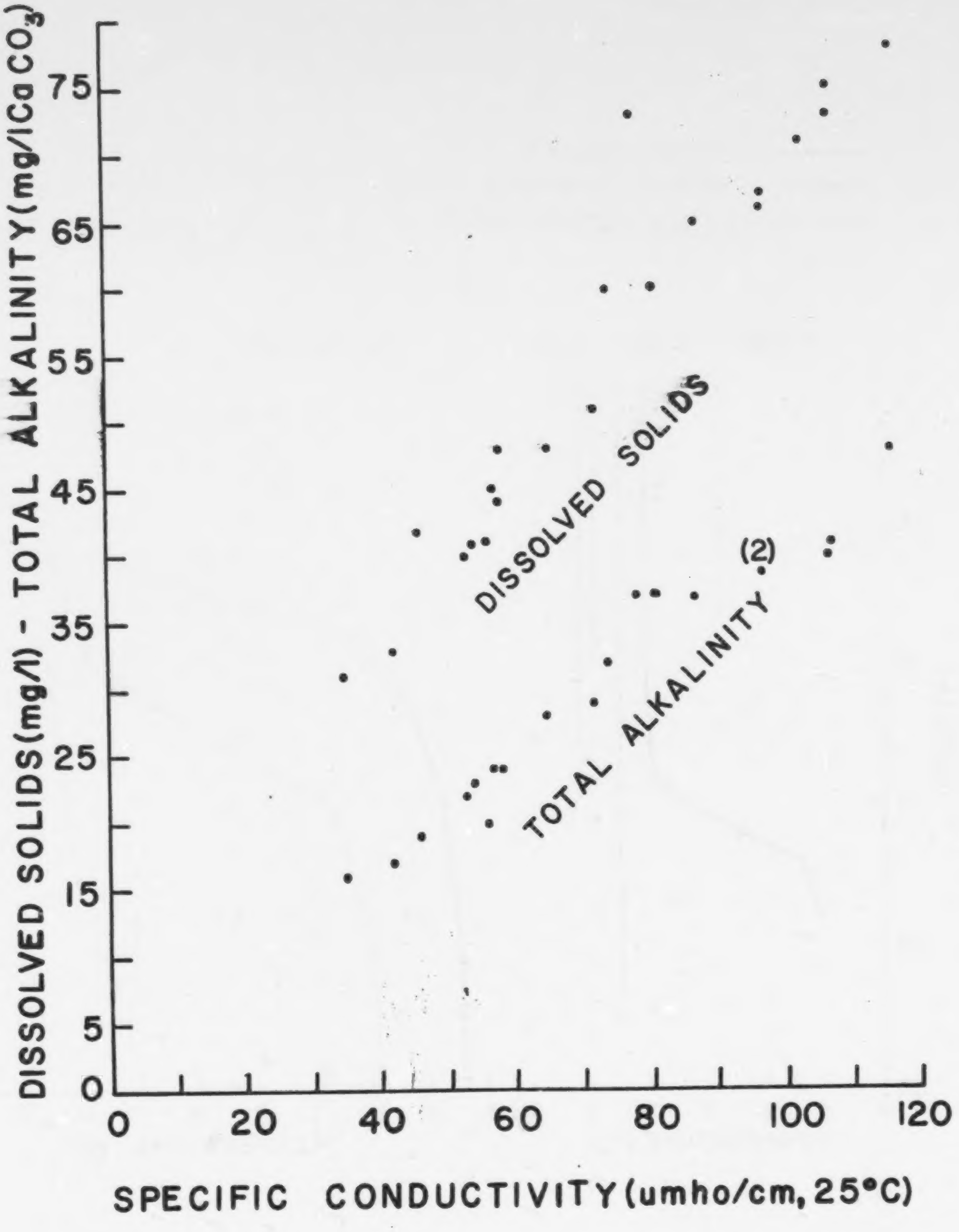

Fig. 3. The relationship between dissolved solids, total alkalinity and conductivity in the waters of the lakes and streams.

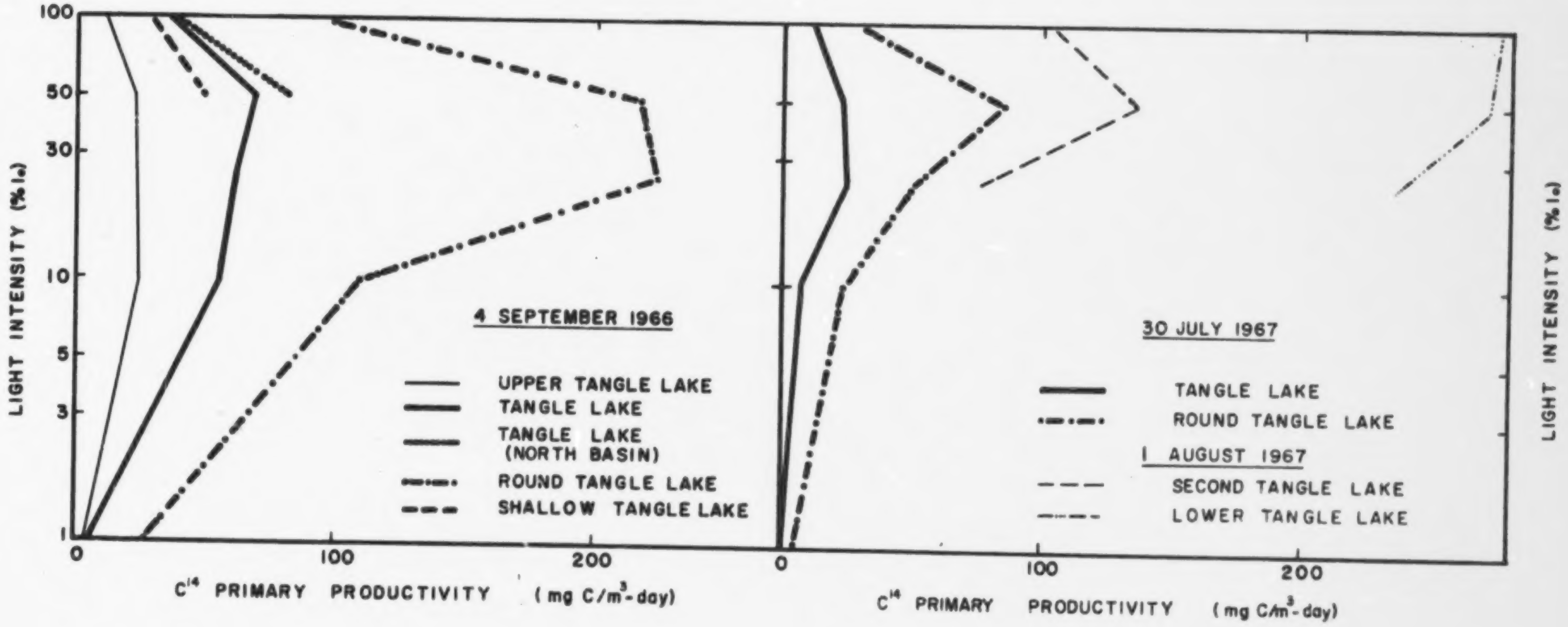

Fig. 4. *In situ* primary productivity in the Tangle Lakes.

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LIMNOLOGICAL STUDIES OF A SUBARCTIC LAKE SYSTEM

By

V. Alexander and R. J. Barsdate

INTRODUCTION

The lakes of interior Alaska are poorly known, since essentially no limnological work had been done in this region until very recently. In order to extend the range of lakes for which information is available, we undertook an investigation of a system consisting of a pair of ~~lakes,~~ Ace and Deuce Lakes. These are small, highly colored lakes located about six miles west of Fairbanks. Some of the morphometric features are shown in Figure 1, and an aerial photograph illustrates the lake situation (Figure 2). As are many lakes of interior Alaska, these appear to be of thermokarst origin, formed by the melting of ice-rich perennially frozen ground.

The methods used in this study were identical to those used in Barsdate and Alexander (1970), and will not be repeated here.

A DISCUSSION OF RESULTS

Thermal

Most of the lakes of interior Alaska go through two periods of thermal instability each year. Since a large portion of the annual heat budget is expended in melting the winter's accumulation of ice, the lakes are not ice-free until late May or early June, when the sun is above the horizon for about 20 hours a day and isolation is approaching its summer maximum. Under these conditions stratification can begin quickly, and in small highly colored lakes it is not uncommon to observe surface temperatures of 7°C or 8°C the day after the lake surface ice disappears. Alternatively, the lakes may mix rather thoroughly for some time, as the course of thermal stratification in the spring is very dependent upon weather conditions. In the fall, the situation is quite different, and the lakes circulate actively for a period of a month or more before the freeze-up in late September or more often in October.

Ace and Deuce Lake do not entirely conform to this pattern. Deuce Lake is meromictic, and never undergoes complete circulation. Ace Lake is also typical of this regional circulation pattern in that the spring circulation is confined to the surface layers and the autumnal mixing, although eventually reaching deep water, is severely attenuated. The annual heat budget for Ace Lake is 11,340 cal/sq. cm., of which the summer budget accounts for 4,180 cal. and the winter 7,160. The melting of the ice accounts for 6,360 of the winter total, or 89% of the winter heat is used to melt the ice. The Deuce Lake annual heat budget is 7,789 cal/sq. cm., of which the summer budget accounts for 2,268 cal. and the winter 5,521 cal. Temperature profiles for Ace and Deuce Lake are shown in Figs. 3, 4, 5 and 6.

Chemical

The incoming waters of Deuce Lake are of two distinct types. The surface runoff water has comparatively low concentrations of dissolved ions and enters the lake through an ephemeral stream. Water with high concentrations of dissolved ions comes from a subsurface source and presumably is a lateral discharge of ground water. The existence of this subsurface input is implied from the sustained flow through the outlet during periods when little or no surface water is entering the lake.

The composition of Ace Lake water reflects a two-component input system. The outlet water which leaves the surface of Deuce Lake runs through a short stream into Ace Lake, where because of its greater density it sinks toward the bottom (Fig. 1). In respect to the major chemical constituents, the deeper waters of Ace Lake are very similar to the surface waters of Deuce. The second component, surface runoff, enters Ace in large volume during the spring breakup and periods of heavy rainfall, since the lake is located on the axis of a relatively large drainage basin.

The ionic composition of the waters of Ace Lake is not radically different from those of other lakes of the surrounding area. Like most of these lakes, it is of the calcium carbonate type, although total quantities of dissolved ions are somewhat higher in Ace Lake. For example, the total of the alkaline earths and carbonate in this lake is about 120 mg/liter, while parallel values for three other lakes in the Tanana Valley (Smith, Birch and Harding Lakes) range from 50 to 80 mg/liter (unpublished data). As is the case in many of the smaller Alaskan lakes, the vertical scale of the physical and chemical structuring in these lakes is compressed. Although Deuce Lake is only 5.6 m deep, the bottom water appears to be permanently anoxic and the major dissolved components can vary by a factor of 4 over a depth interval of 2 m. The distribution of dissolved solids in Ace Lake shows that although there is some effect of spring mixing, Ace Lake remains chemically stratified during the vernal circulation (Fig. 7). The temperature profiles shown above, as well as the oxygen profiles (Figs. 8 & 9) show the intensity of the stratification. Both of the lakes tend to be depleted in oxygen below the surface throughout the entire year, and traces of hydrogen sulfide are apparent in the oxygen-free water. Ace and Deuce Lakes are relatively high in nutrient content, although some reduction of levels in the epilimnion is evident in Ace Lake during the summer (Tables 1 & 2). Such depletion never reaches severe proportions. These nutrient levels are substantially higher than those found in many other lakes in this region.

Plant Productivity

Primary productivity was measured using carbon-14, with *in situ* incubation. There appears to be no well-defined pattern in the results (Fig. 10). Spring blooms in the second week of June are often striking features of the annual productivity cycles of interior Alaskan lakes, and here, although the highest photosynthetic rates occurred early in the summer, the peak is very transient and occurs earlier than the typical spring bloom. The total productivity expressed on a unit surface area basis shown in Fig. 11, indicates productivity sustained at rather high levels throughout the summer without showing marked blooms.

A diurnal productivity study was undertaken in the open water of the moat surrounding the ice of Ace Lake during the break-up period, and the results of the diurnal indicate that the efficiency of conversion of sunlight into assimilated carbon was much higher during the period between 4 a.m. and 8 a.m. than during the remainder of the day (Fig. 12).

Insufficient data are available for Deuce Lake to draw conclusions on the seasonal behaviour of this lake (Fig. 13). However, extreme variation is evident, possibly due to variable conditions such as wind stress, advection, etc. For example, at the time of the August 6 maximum, nutrient levels were reduced to a somewhat greater depth than on most occasions, suggesting that mixing had provided a higher level of nutrient availability. The apparent dynamic range is very much greater than in Ace Lake. On the few occasions when simultaneous experiments were carried out on both lakes, Deuce Lake invariably showed higher photosynthetic rates. This is reflected in the relative plant pigment concentrations between the two lakes.

Surface chlorophyll *a* levels are consistently high compared with other lakes in the area. Extractable pigments at depth tend to increase with depth in both lakes, although there is a peak shift in the acetone extracts in samples from below the zero oxygen depth level in Ace Lake (Fig. 14). The nature of the pigment or pigments involved has not yet been determined. The absorbance of the pigment is very high and in the absence of identification we have arbitrarily reported it as chlorophyll *a*. The seasonal plot for Ace Lake clearly indicates extremely high summer pigment maximum at three meters, and also the buildup of rather high pigment levels in the deeper water at 5 and 7 m (Fig. 15). The chlorophyll maximum correlates with the thermocline, as does the disappearance of oxygen (Fig. 15). The mean depth of 1% of incident light was 1.3 m, with an extinction coefficient of 3.5/m. One month later, there was a sizeable increase in the proportion of the pigment at greater depths (Fig. 16) and this continued to increase during the summer.

Chlorophyll levels tend to be considerably higher in the surface waters of Deuce than in Ace, and very much higher in the deeper waters (Fig. 17). The attenuation of light is even more pronounced in Deuce than in Ace Lake, and the mean depth of 1% surface illumination is 0.8 m, with an extinction coefficient of 5.9/m. The high extinction coefficients in these lakes are not due primarily to sestonic components, but to the presence of large quantities of highly colored organic acids (over 1,000 platinum units in the surface waters of Deuce Lake, and over 400 in the surface waters of Ace Lake).

Although a well-defined spring bloom was not apparent from the productivity data, a substantial peak in particulate nitrogen occurred in the surface water of Ace Lake, extending down to 3 m in late May (Fig. 18). Rather high values also occurred during July. These were also reflected in the chlorophyll data (Fig. 19). The deeper waters show a clearly developed seasonal cycle of particulate nitrogen, with maxima in mid-summer of about 15 ug-at/l.

There are two opposing factors in productivity here: the high light absorption by the colored water, and the high nutrient levels associated with the meromictic character of these lakes. Even though productivity is negligible at depths greater than a meter, the annual carbon assimilation is quite high for the latitude, over 70 g C/m^2-yr. In comparison, a small lake in the same area produced only about 10 g C/m^2-yr. Imikpuk Lake, a truly arctic lake, fixed 8.4 g C/m^2-yr. according to Kalff (1967), and Hobbie's (1960) values for Lake Schraeder suggested 7 g for the annual production. Although not a highly productive lake by temperate standards, Ace Lake production is surprisingly high in view of the light conditions and the short length of the growing season.

SUMMARY

Data have been presented describing a small two-lake system in subarctic Alaska.

These lakes have strongly meromictic tendencies, are composed of highly colored water with a rather high ionic content. The phytoplankton productivity of these lakes is surprisingly high for the geographical region.

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Table I

Ace Lake Nutrients (µg-at./liter)

	NH_3-N				NO_3^--N			
Depth (m)	Winter	Spring	Summer	Fall (mixing)	Winter	Spring	Summer	Fall
0.0	Ice	6.4	2.7	10.6	Ice	1.4	0.6	2.2
1.0	11.2	8.2	2.3	10.2	2.2	2.2	0.5	2.3
3.0	13.9	16.2	3.4	8.0	1.9	2.1	1.5	2.8
5.0-7.0	41.0	36.5	14.2	12.4	1.9	2.0	1.7	7.0

	NO_2^--N				PO_4^{3-}-P			
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
0.0	Ice	0.0	0.2	0.2	Ice	1.5	0.6	2.2
1.0	0.16	0.1	0.2	0.4	2.7	5.2	0.8	2.1
3.0	0.28	0.2	0.5	0.4	3.7	4.9	4.6	2.5
5.0-7.0	0.30	0.4	0.9	0.6	13.8	13.7	10.2	3.4

	$Si(OH)_4$-Si			
	Winter	Spring	Summer	Fall
0.0	Ice	76	66	141
1.0	87	75	51	52
3.0	91	77	75	53
5.0-7.0	137	112	119	66

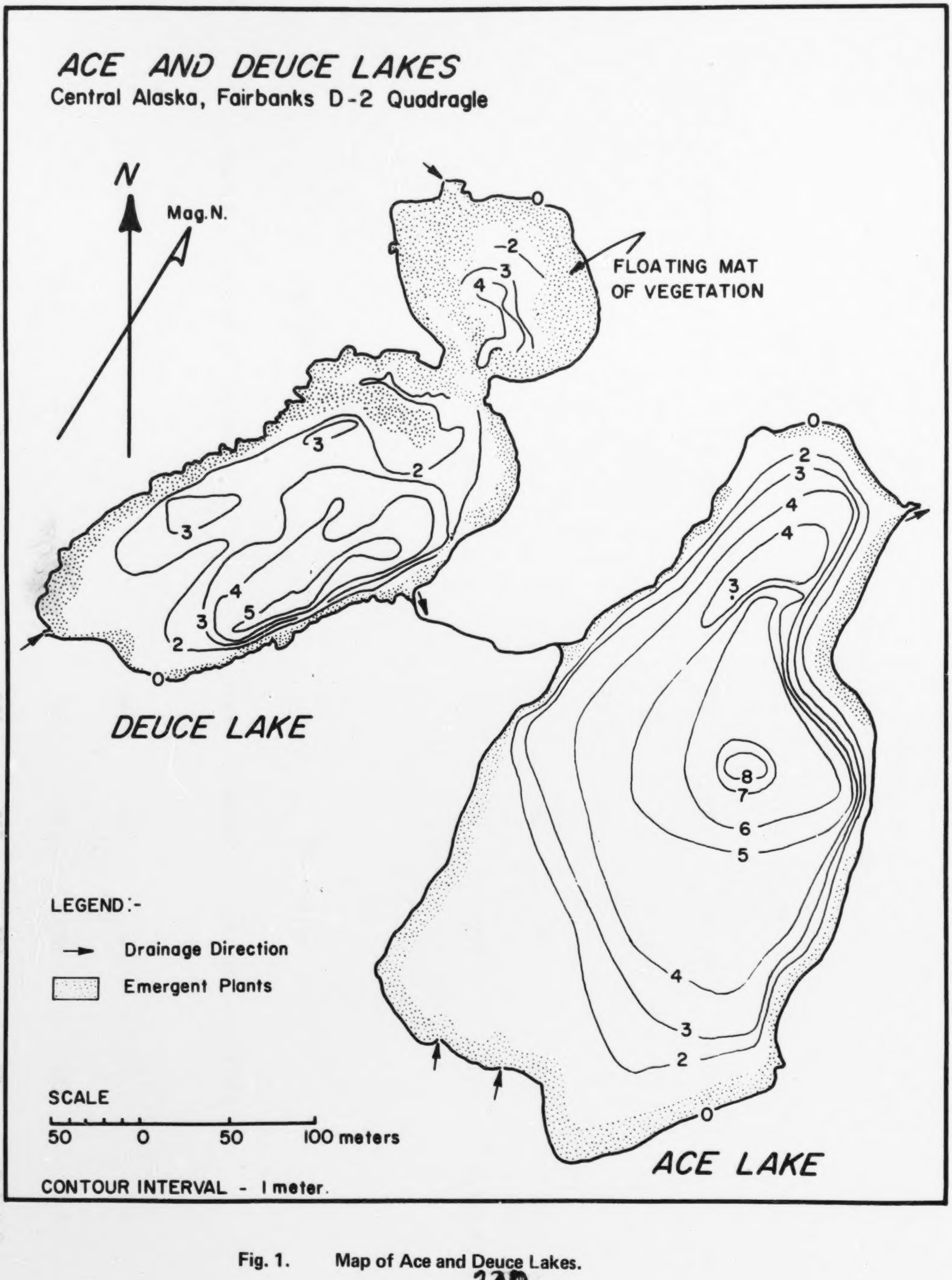
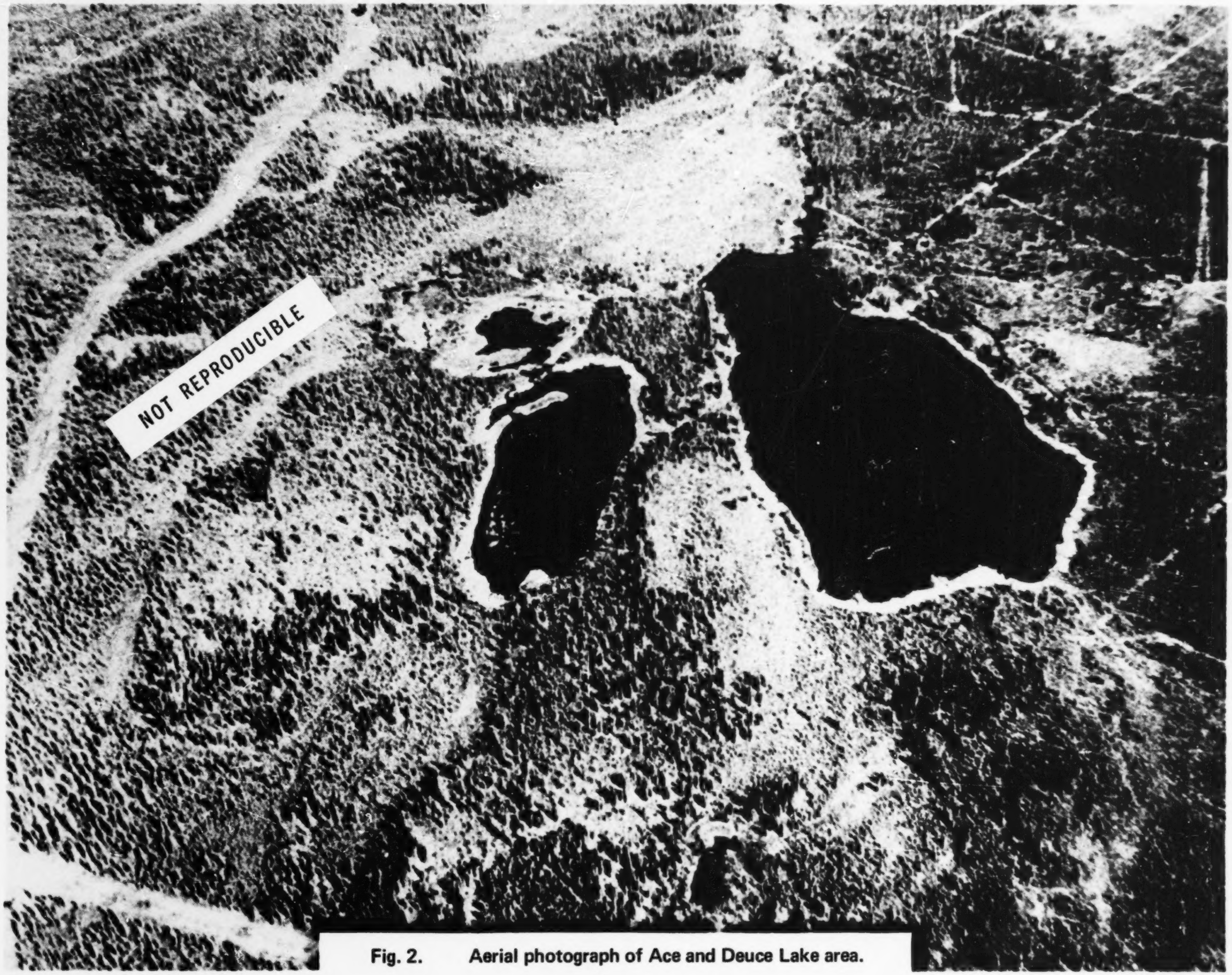

ACE AND DEUCE LAKES
Central Alaska, Fairbanks D-2 Quadragle
N
Mag. N.
FLOATING MAT OF VEGETATION
DEUCE LAKE
ACE LAKE
0
2
3
4
5
6
7
8
LEGEND:-
Drainage Direction
Emergent Plants
SCALE
50
0
50
100 meters
CONTOUR INTERVAL - 1 meter.

Fig. 1. Map of Ace and Deuce Lakes.

Table 2
Deuce Lake Nutrients (μg-at./liter)

	NH_3-N				NO_3^--N			
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
0.0	-	-	10	65	-	-	5.0	2.5
1.0	63	92	38	70	5.0	5.0	2.0	3.2
2.0-4.0	76	125	90	100	5.0	5.0	2.0	2.4

	$Si(OH)_4$-Si				PO_4^{3-}-P		
	Winter	Spring	Summer	Fall	Winter	Spring	Summer
0.0	-	-	165	240	-	-	1.0
1.0	220	360	170	235	9.2	8.9	1.5
2.0-4.0	90	170	200	153	15	14.4	1.2



NOT REPRODUCIBLE

Fig. 2. Aerial photograph of Ace and Deuce Lake area.

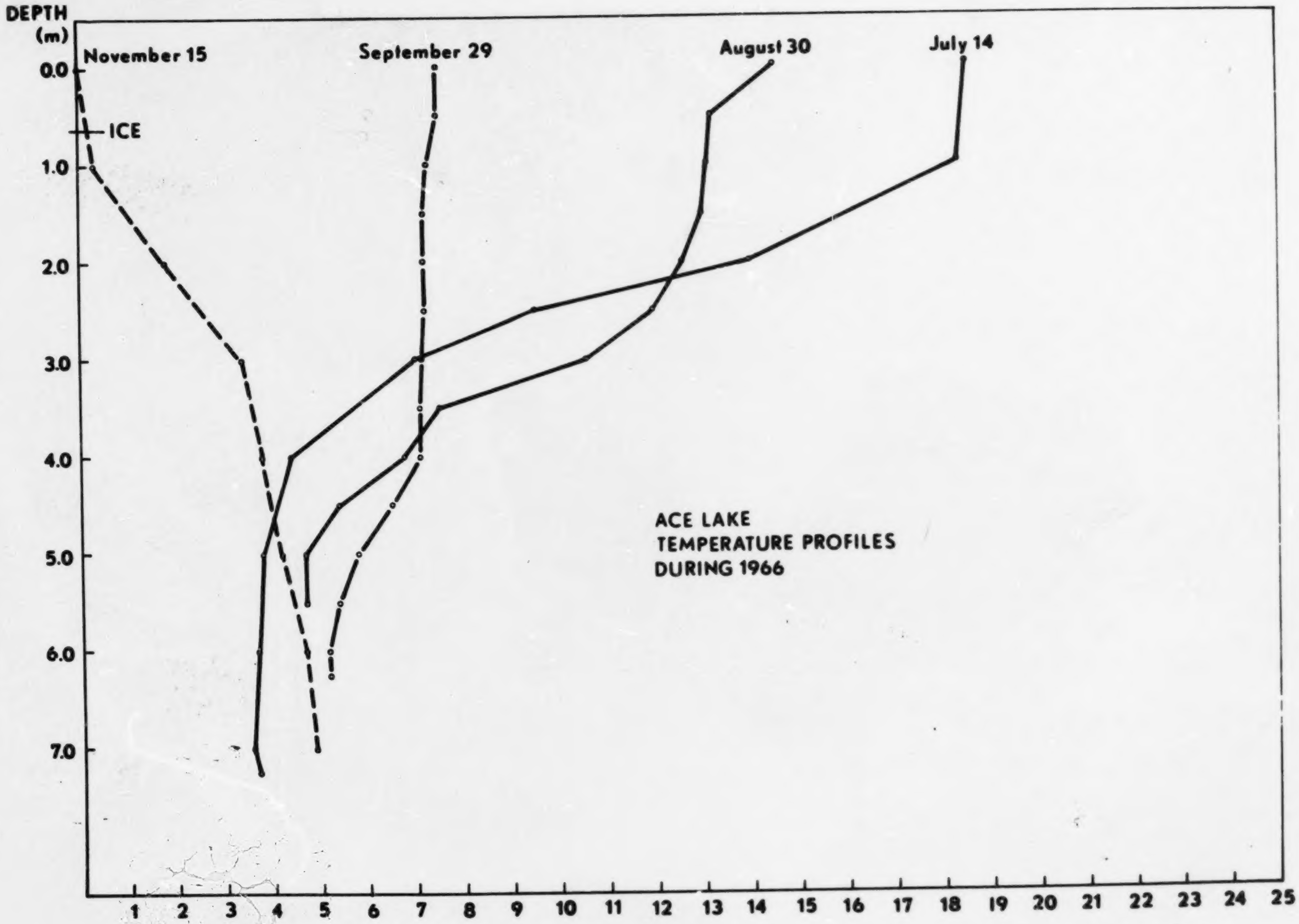


Fig. 3. Ace Lake temperature profiles, 1966.

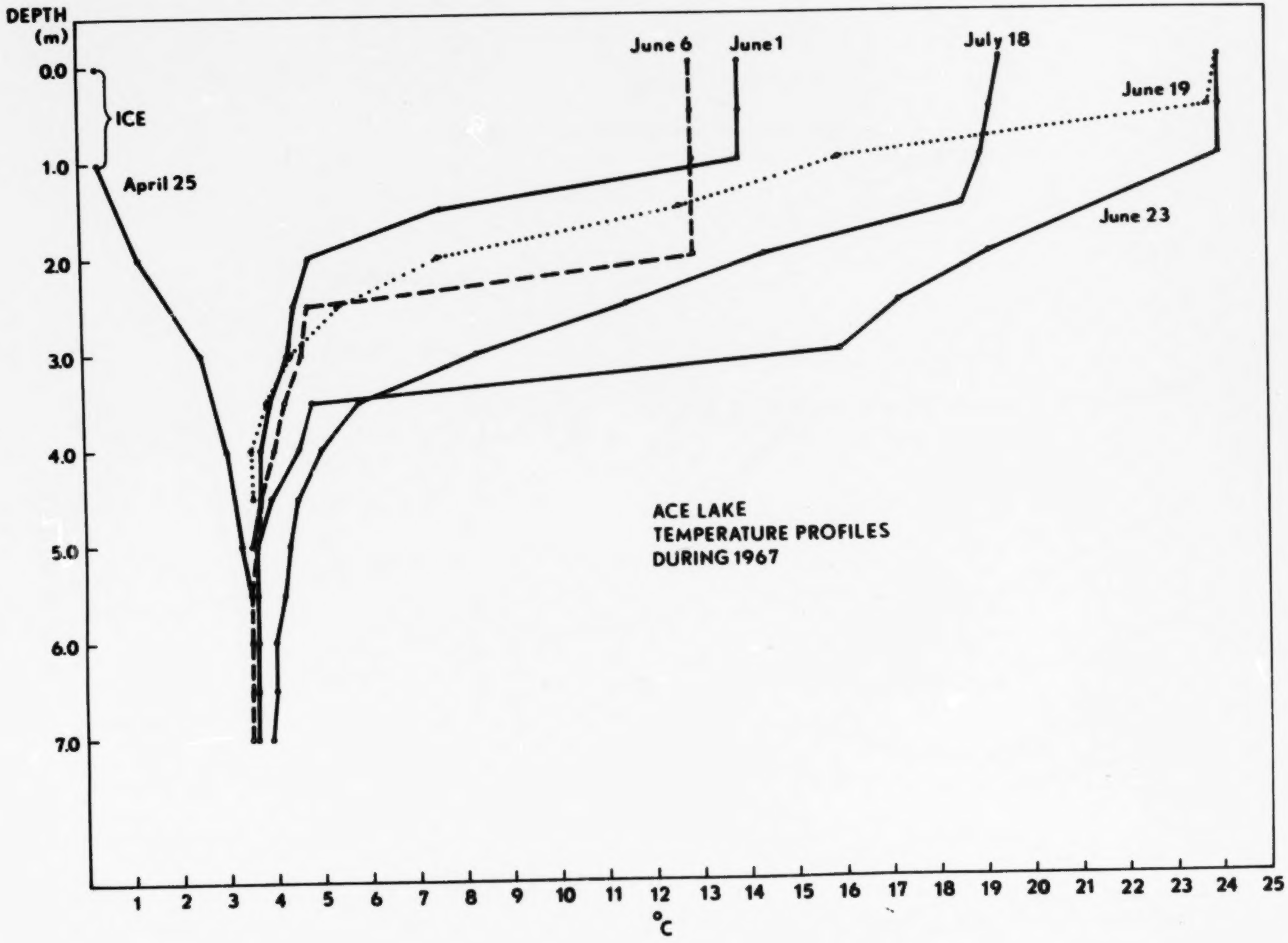


Fig. 4. Ace Lake temperature profiles, 1967.

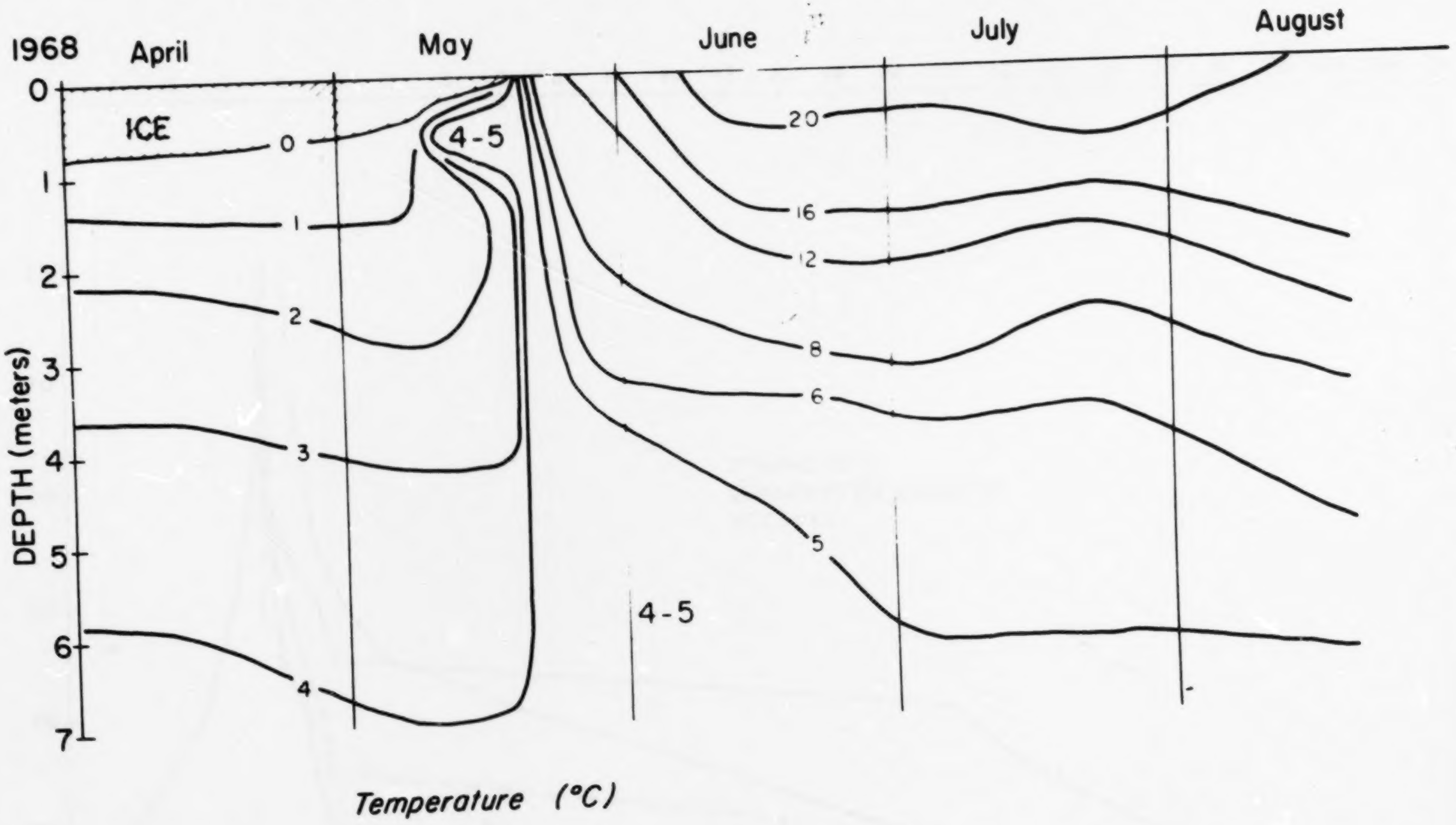


Fig. 5. Ace Lake temperature data, 1968.

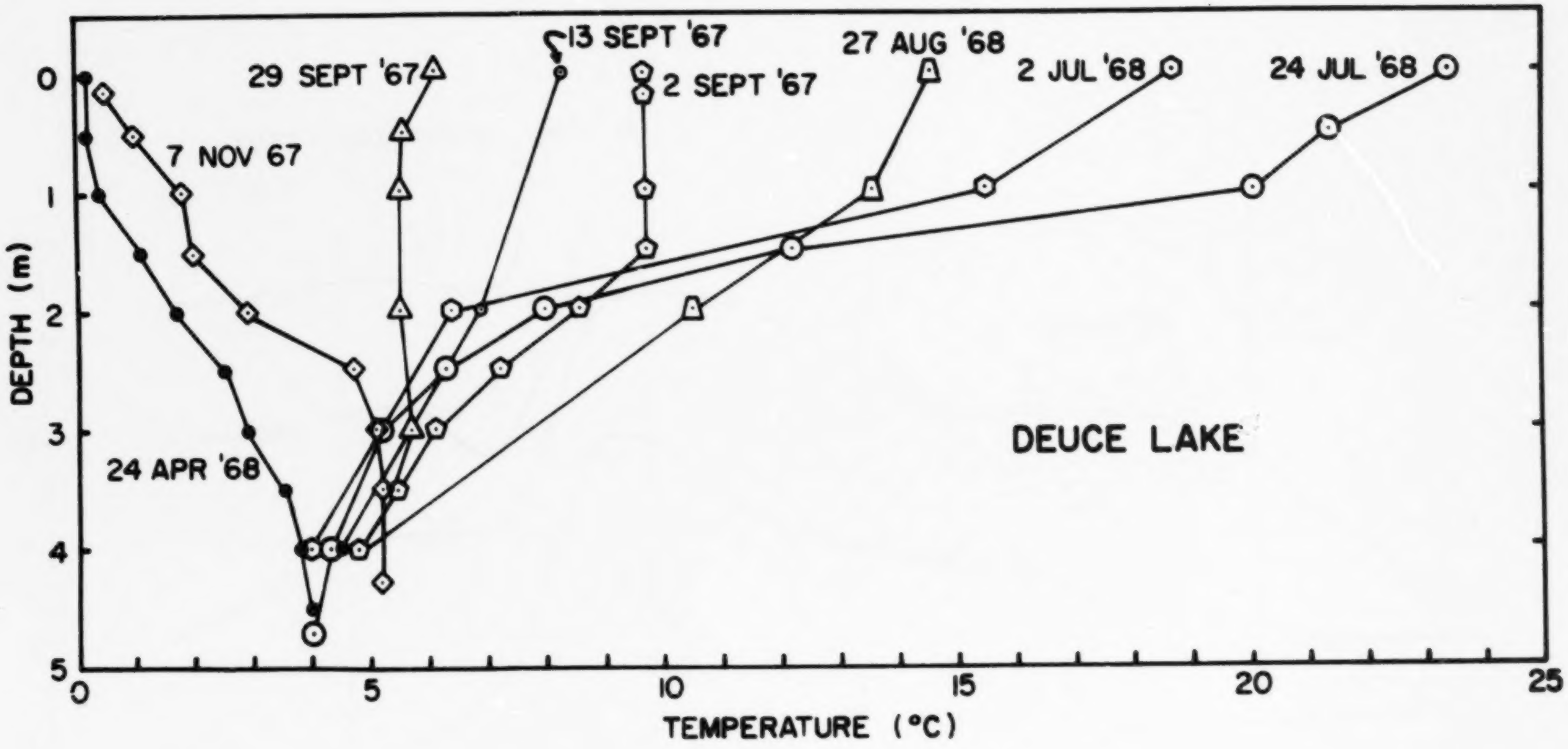


Fig. 6. Deuce Lake temperature profiles.

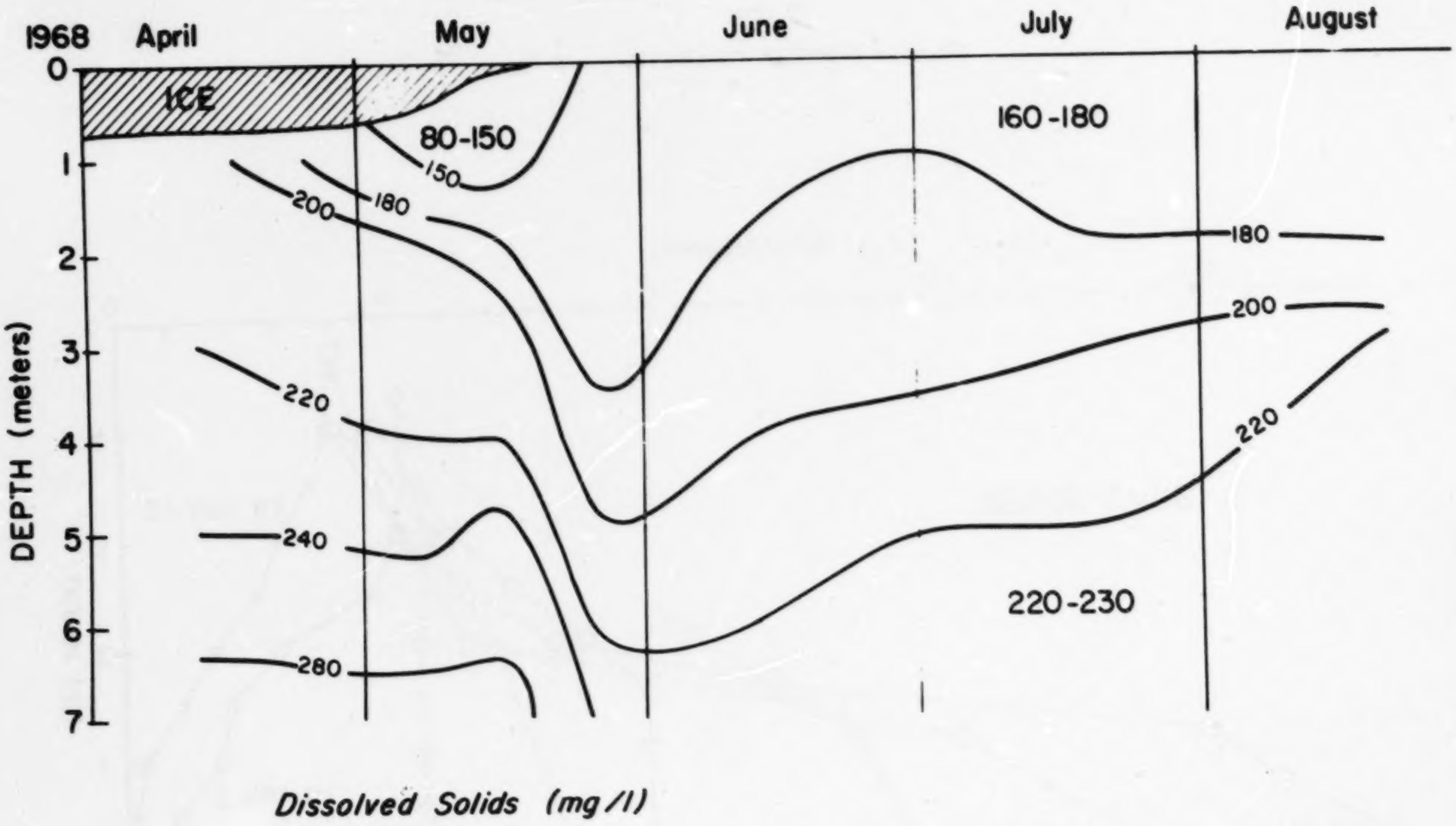


Fig. 7. Total dissolved solids, Ace Lake.

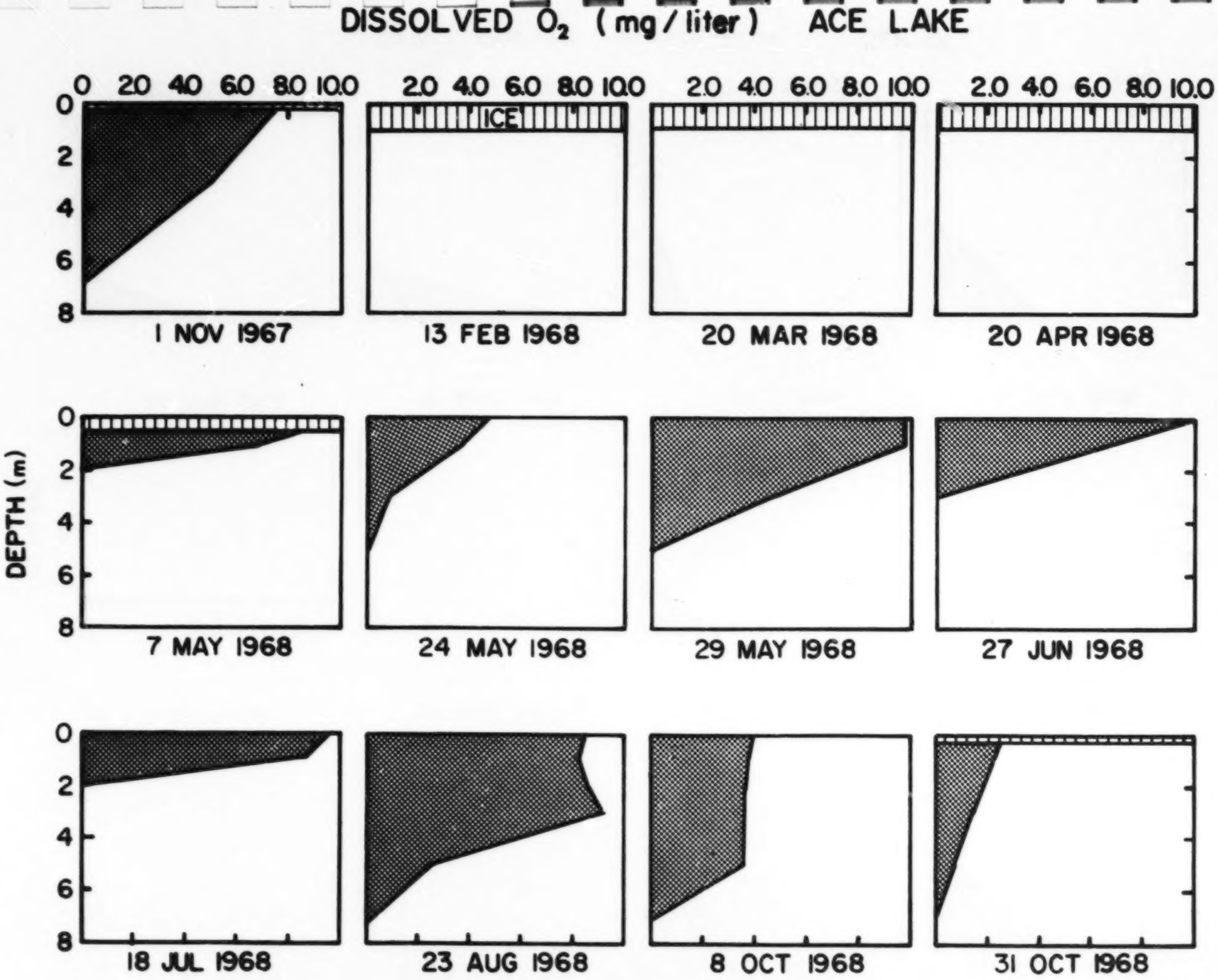


Fig. 8. Dissolved O_2 (mg/liter) Ace Lake.

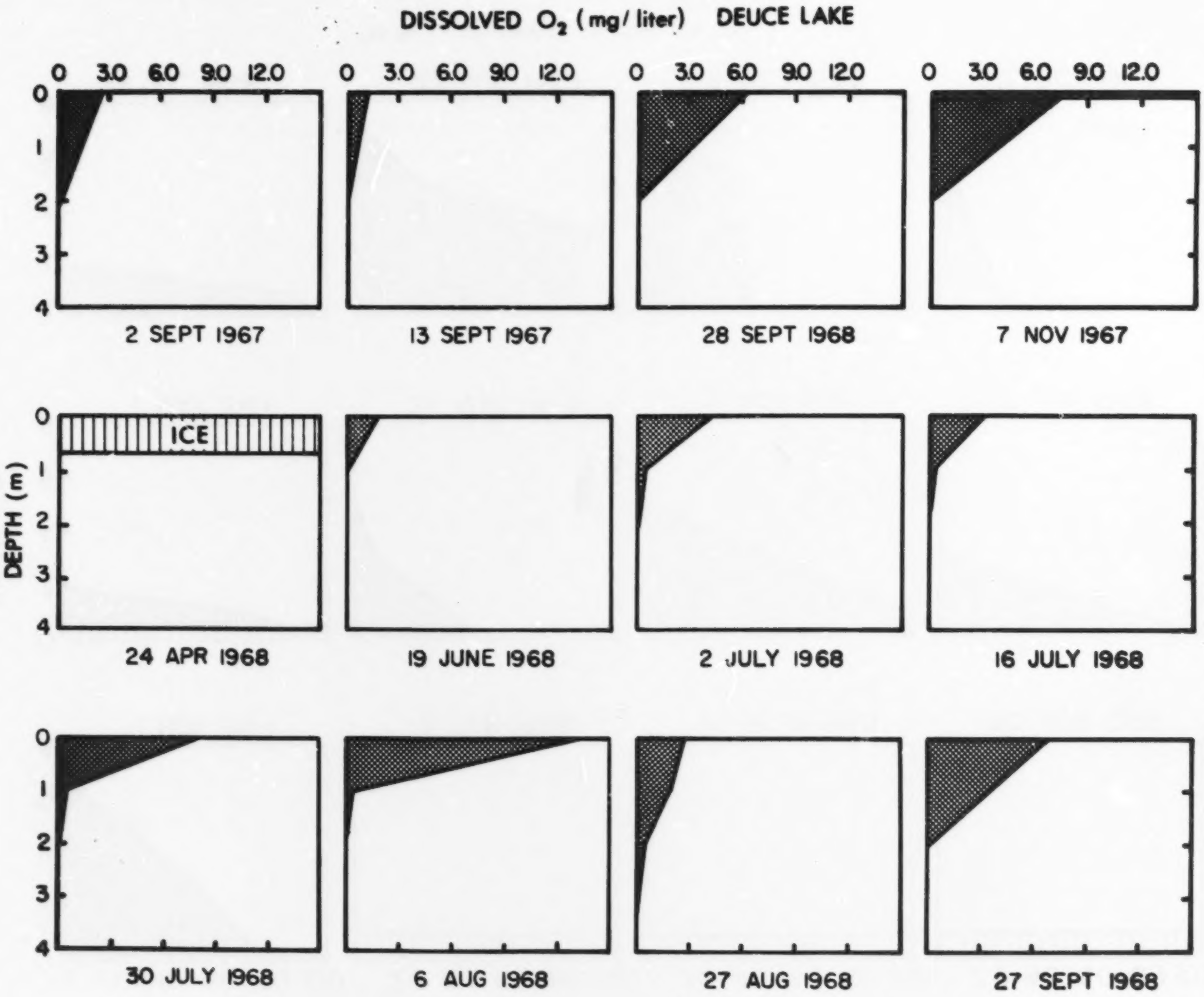


Fig. 9. Dissolved O_2 (mg/liter) Deuce Lake.

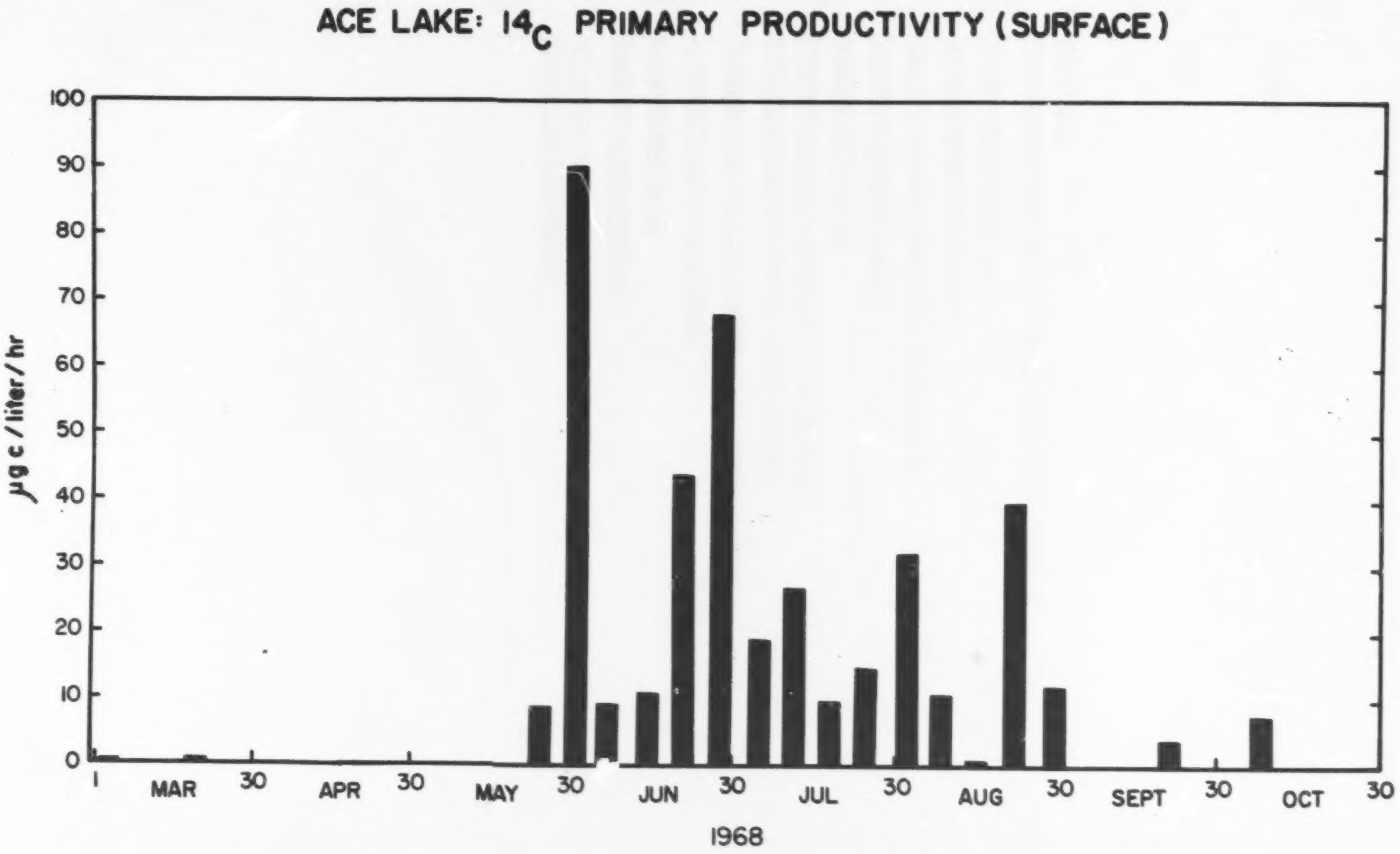


Fig. 10. Ace Lake: ^{14}C primary productivity (surface).

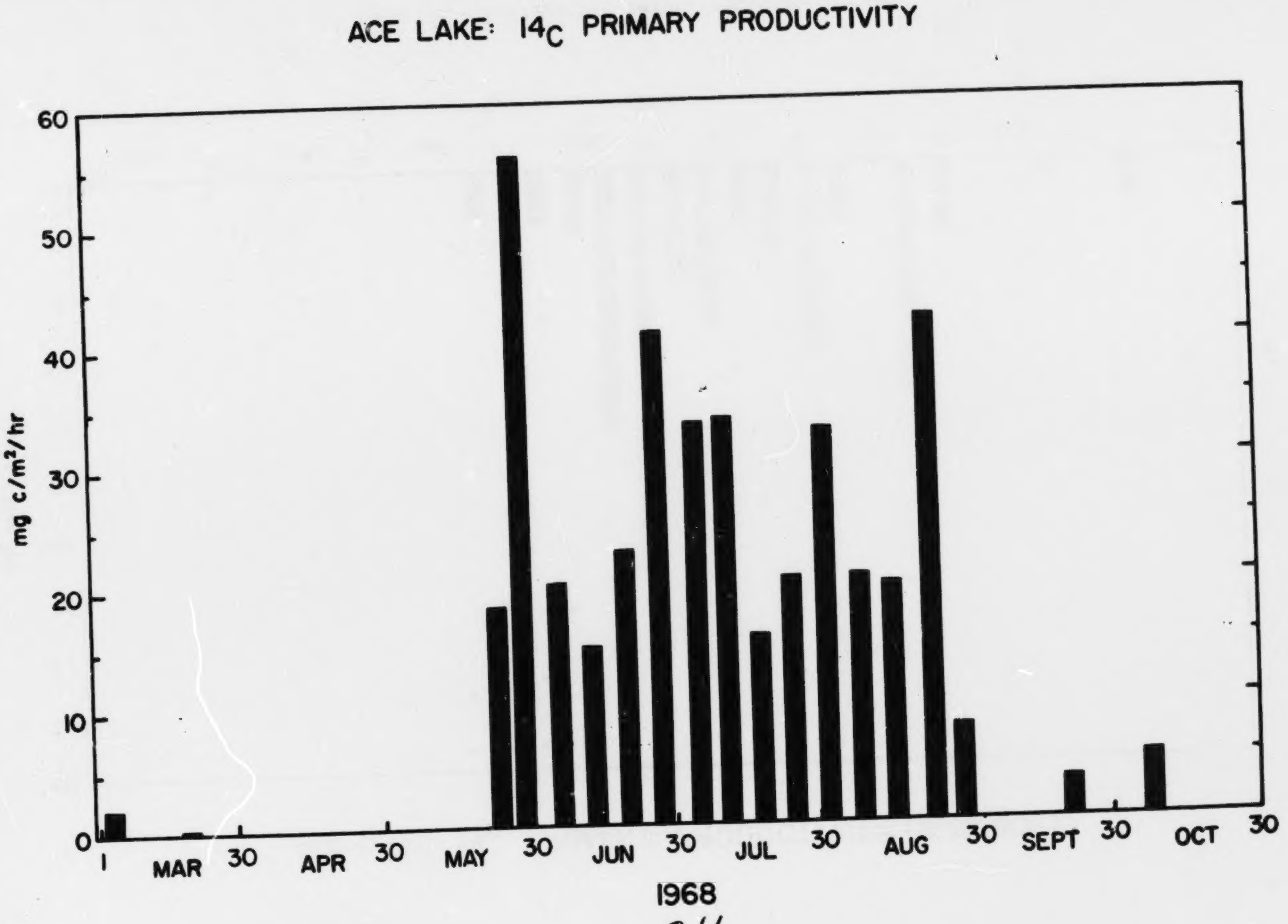


Fig. 11. Ace Lake: ^{14}C primary productivity

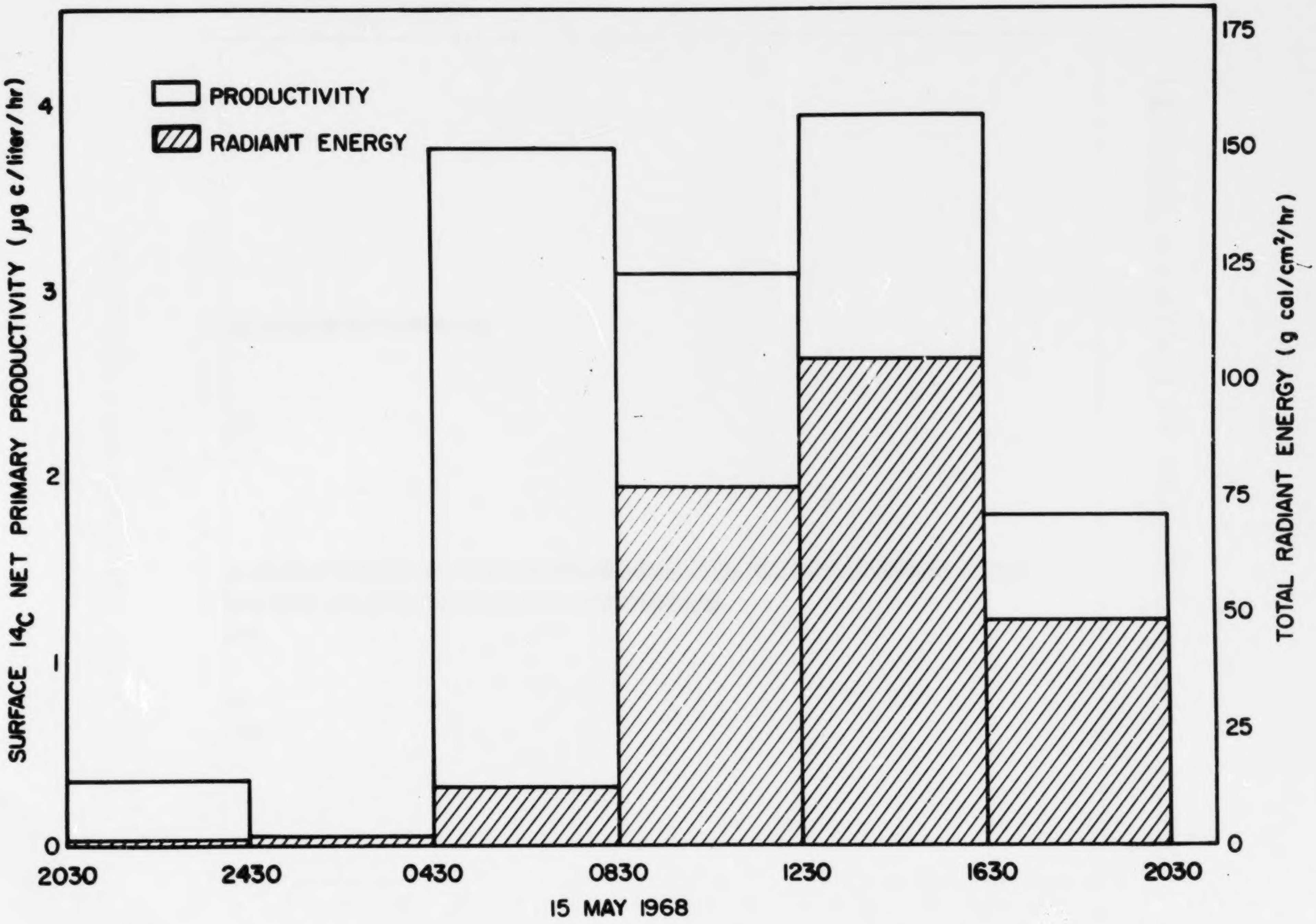


Fig. 12. Diurnal primary productivity in Ace Lake.

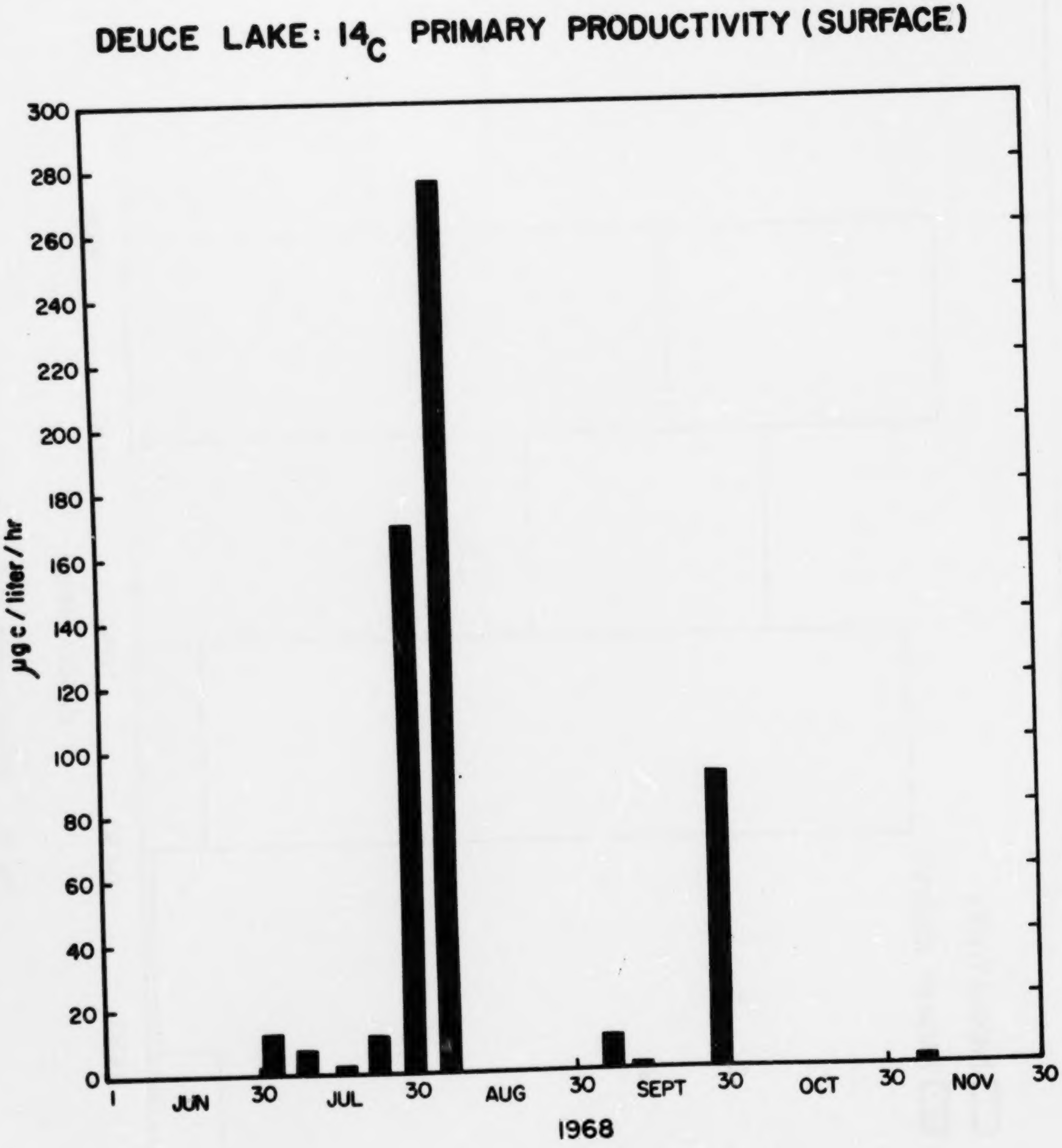


Fig. 13. Deuce Lake primary productivity results.

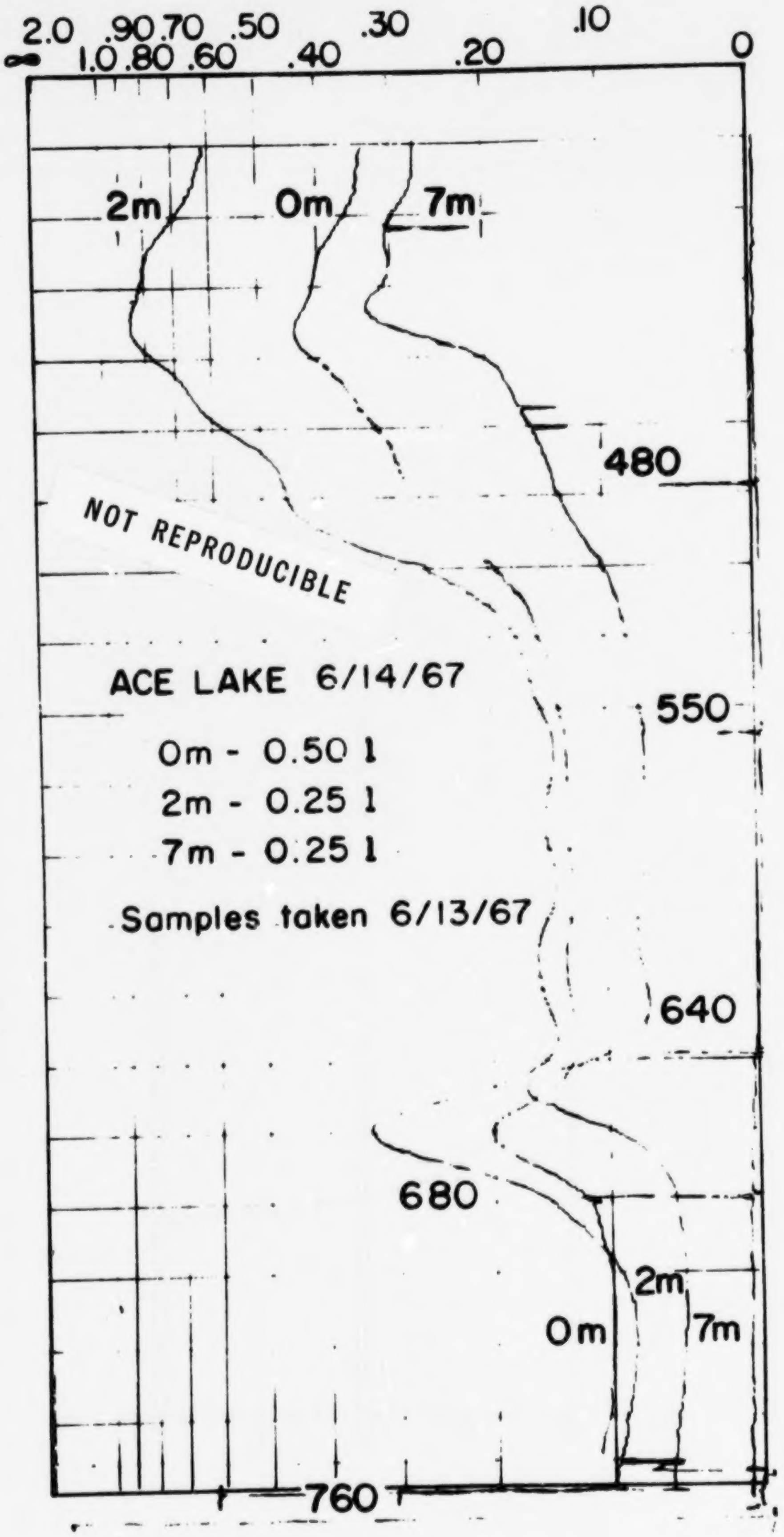


Fig. 14. Chlorophyll extract scars for different depths - Ace Lake.

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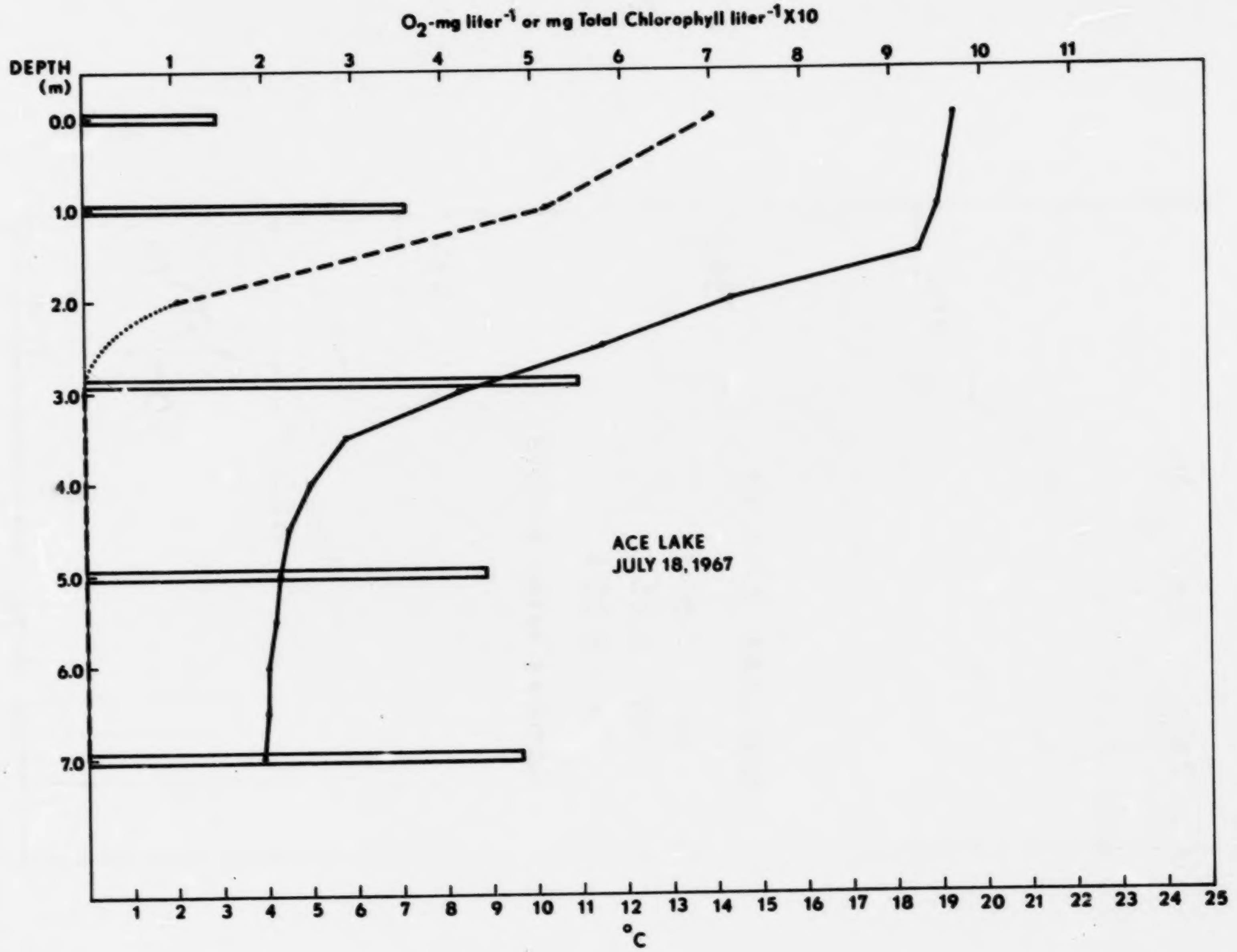

Fig. 15. Oxygen and temperature profiles with chlorophyll for Ace Lake.

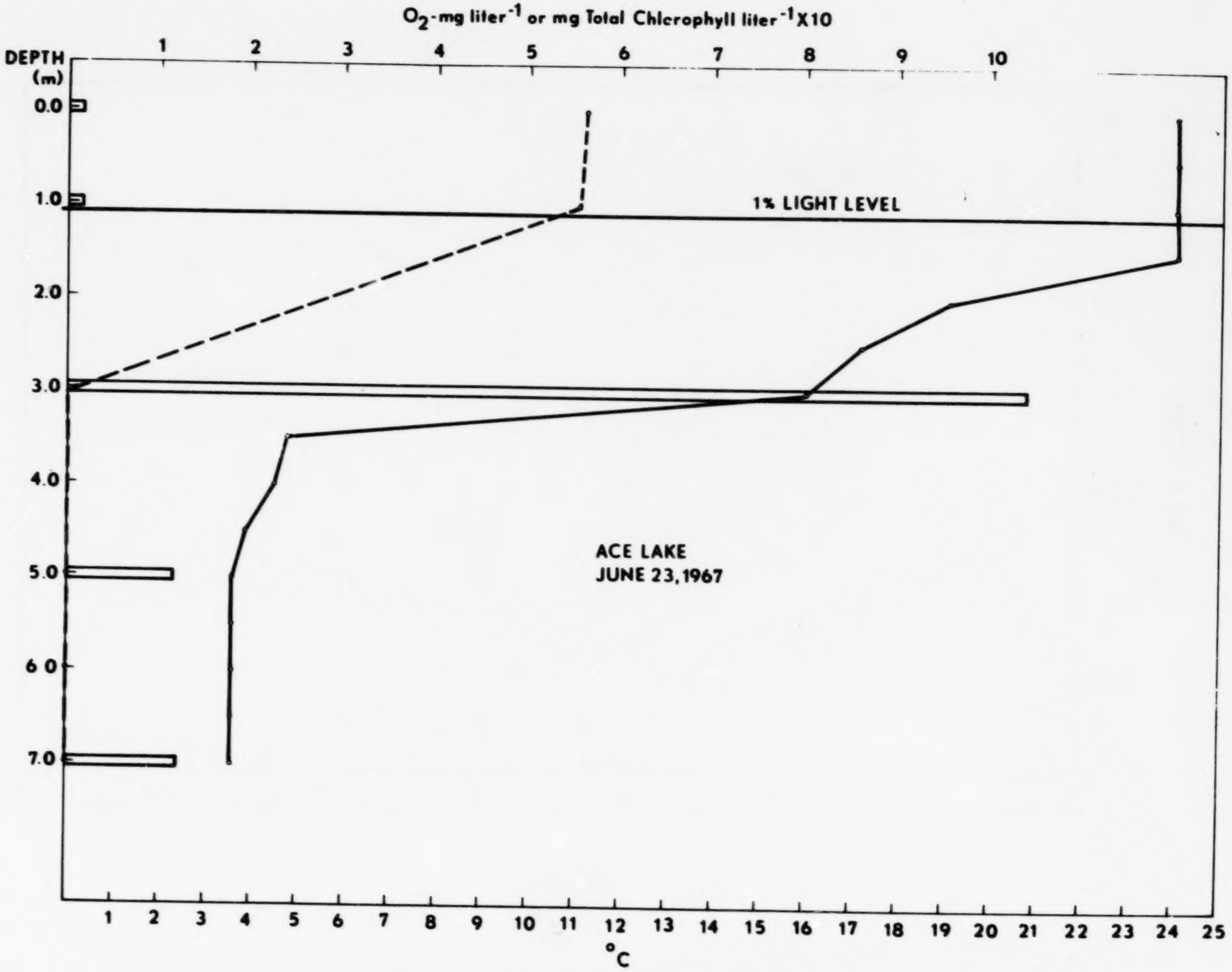

Fig. 16. Oxygen, temperature, chlorophyll and 1% light penetration depth - Ace Lake.

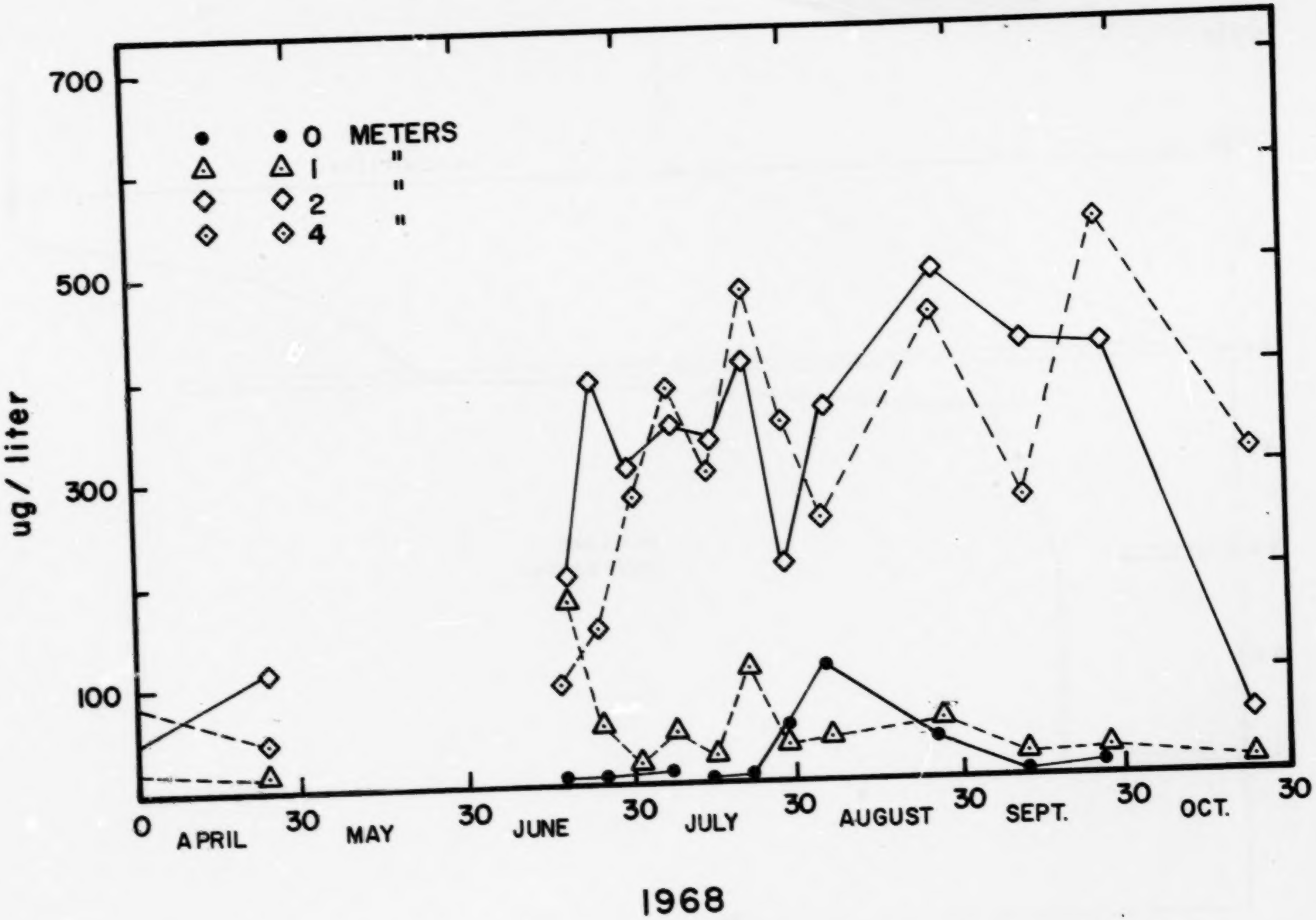

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Fig. 17. Chlorophyll data, Deuce Lake 1968.

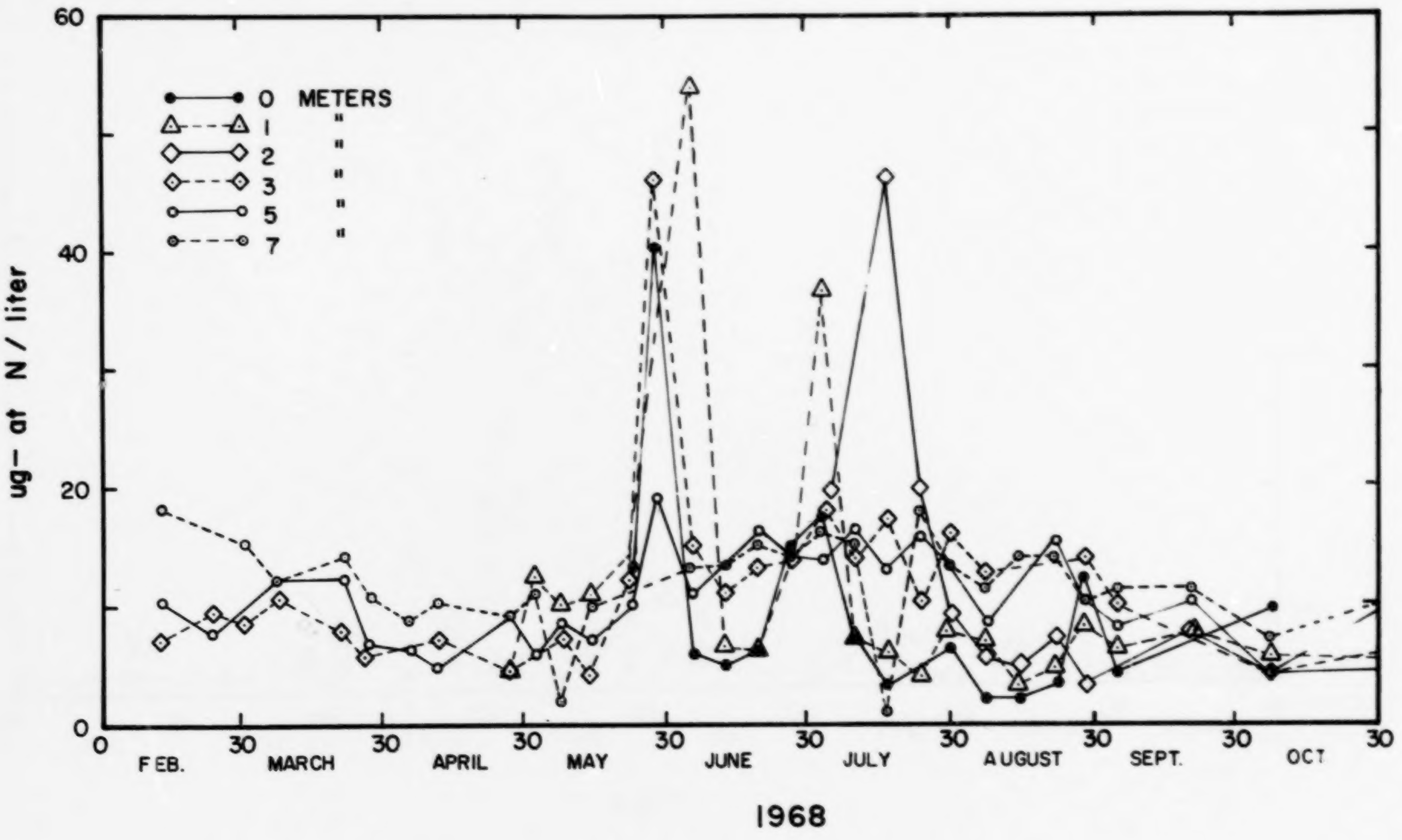

Fig. 18. Particulate nitrogen, Ace Lake 1968.

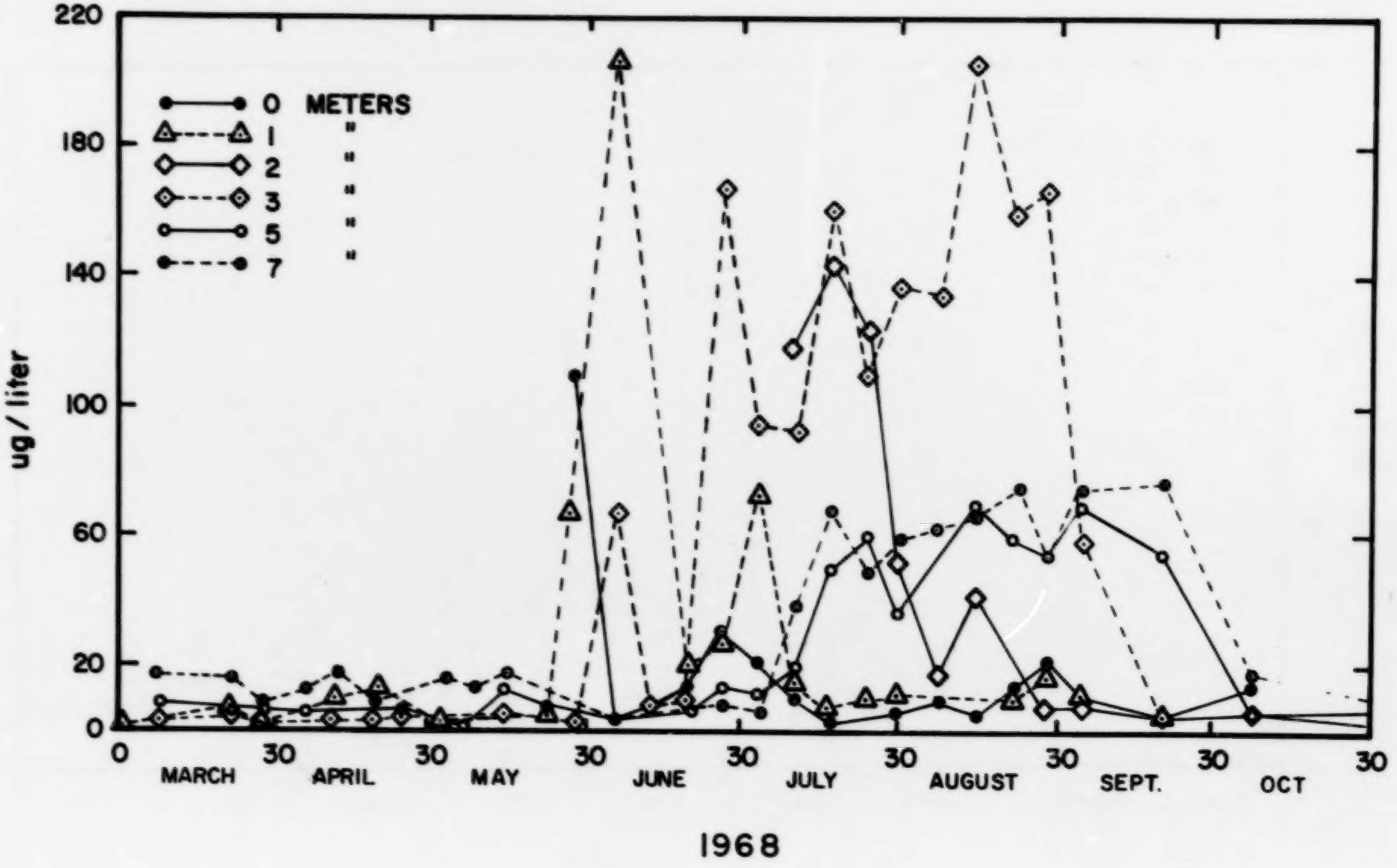

Fig. 19. Chlorophyll data, Ace Lake 1968.